ELEMENTS of BOTANY

RICHARD M. HOLMAN ~ WILFRED W. ROBBINS

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ELEMENTS OF BOTANY

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By RICHARD M. HOLMAN, Late Associate Professor of Botany in the College of Letters and Science of the University of California; and WILFRED W. ROBBINS, Professor of Botany in the College of Agriculture of the University of California. Third Edition, 392 pages. 6 by 9¼. 273 figures. Cloth.

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LABORATORY GUIDE FOR A COURSE IN GENERAL BOTANY

By LEE BONAR, Associate Professor of Botany in the University of California, LUCILE ROUSH, of the Department of Biological Science, Mills College, and the late RICHARD M. HOLMAN. Fourth Edition, 110 pages. 6 by 9¼. Cloth.

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BY

RICHARD M. HOLMAN

Late Associate Professor of Botany in the College of Letters and Science of the University of California

AND

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Professor of Botany in the College of Agriculture of the University of California

THIRD EDITION
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AND
WILFRED W. ROBBINS

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PREFACE TO THIRD EDITION

Since the date of publication of the second edition of this book, its companion, "A Textbook of General Botany for Colleges and Universities," has gone through two editions, these appearing in 1934 and 1938. In the preparation of this third edition of "Elements of Botany" it has seemed wise to adhere to the organization and viewpoint of preceding editions; in these particulars the two textbooks are very similar. Accordingly, such changes as have appeared in the last two editions of the "Textbook" are incorporated in this edition of "Elements of Botany." These changes involve factual material, especially in physiology, and illustrations.

Considerable attention has been given to applications and items of general interest. Such material, for the most part, is set in fine print. Mention is made at logical places of such topics as the rôle of growth substances and their use in agricultural practice, "hydroponics" or water-culture methods of growing plants, root systems in relation to soil erosion, methods used in altering the duration of the life cycle of plants, artificial pollination, self-sterility in commercial fruit varieties, efficiency of certain plants in the production of carbohydrates, economic importance of plant diseases, principles of control of the classes of weeds, economic value of certain plants and of various plant products, such as cellulose, alkaloids, glucosides, oils, latex, sugar, starch, and proteins, "hardening" of plants, "short-day" and "long-day" plants, and methods employed to induce chromosome changes.

Wilfred W. Robbins

Davis, California
May 11, 1940

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PREFACE TO THE SECOND EDITION

The changes embodied in the new edition of this book are based upon the experience of the authors in their own elementary classes in botany since the appearance of the first edition and upon the advice and suggestions which they sought and received from teachers, throughout the country, who have used the book in their own classes. Although considerable changes have been made in every chapter, the organization and point of view have remained the same. Wherever possible without sacrificing the logical organization and clarity of statement which both the thoughtful teacher and the intelligent student recognize as the most essential properties of a good textbook, the authors have sought to increase the ease with which the book may be read.

In its organization the revised edition differs from the original book principally in that an introductory chapter has been added and that the material formerly included in the chapter entitled "The Principal Plant Groups" has been incorporated in other chapters. A number of illustrations have been redrawn and about thirty new cuts added. The text material has been considerably increased, so that in spite of having a larger page the present book contains a few more pages than the first edition.

The authors gratefully acknowledge the helpful suggestions received from teachers in various American colleges and the assistance given them by their associates in the preparation of the revision for the printer.

Richard M. Holman.
Wilfred W. Robbins.

Berkeley, California,
April 28, 1933.

PREFACE TO FIRST EDITION

In August, 1924, the authors published "A Textbook of General Botany for Colleges and Universities," which was designed for a year's course. The Second Edition of this text came from the press in October, 1927. Since the issuance of this book, there has arisen a need for a text which would embody the same material, the same organization and viewpoint as that of the "Textbook of General Botany," but so abridged as to fit it especially for use in institutions in which only one semester is devoted to the course in general botany, or in which, for other reasons, the subject is less extensively studied than in those colleges and universities for which the larger book is particularly fitted. The authors have attempted to meet this need by the preparation of the present book.

A number of illustrations have been borrowed from various sources and are acknowledged in the legends.

Richard M. Holman.
Wilfred W. Robbins.

Berkeley, California,
May 11, 1928.

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ELEMENTS OF BOTANY

CHAPTER I

INTRODUCTION

Man is dependent upon plants for his very existence on the earth. From plants he secures food, shelter, and materials (cotton and linen) for clothing; some plants yield drugs of considerable medicinal value; others furnish such important commercial products as cork, resins, turpentine, dyes, oils, gums, and rubber; and still others are used to adorn our homes, gardens, and parks. All our fuel is of plant origin—coal being ancient vegetation variously modified through partial decay, pressure, and heat, and petroleum, also, being of plant origin.

The truth and the significance of the statement that the very life of man depends upon the activity of green plants are even better realized when we understand that only green plants possess the power of storing the energy of the light of the sun (which is the one great source of energy for our earth) in food and in fuel.

The food of all such non-green plants as bacteria, molds, mildews, and other fungi and the food of all animals are derived directly or indirectly from green plants. The land animals used by man as food and as beasts of burden are herbivorous; that is, they live upon plants. The food of fishes is chiefly the innumerable microscopic aquatic animals, which in turn gain their sustenance from microscopic free-floating aquatic plants.

The great civilizations of the world have developed where natural conditions favored the cultivation of certain food plants, chiefly cereals. Rice, wheat, corn—these have been the three most important food plants which have made possible the development of three great civilizations: (1) that which spread over eastern Asia, Japan, the Indian Archipelago, the Malay Peninsula, and the

Philippine Islands was dependent upon rice; (2) that which developed in western Asia, northern Africa, and Europe depended upon wheat and related cereals as the chief food plants; and (3) the civilization of the Mayas, Aztecs, Incas, Guatemalans, Peruvians, and other American peoples depended upon maize or Indian corn.

The three cereals mentioned above, namely, rice, wheat, and corn, are members of the grass family (*Gramineae*). Of all the families of plants, grasses have played the most important part in the development of the civilizations of the world; of all plants they are of the greatest use to the human race. Cereals, including rice, wheat, corn, barley, rye, and grain sorghums, are the most important food plants for human beings. Grasses constitute the main plant growth of meadows and pastures and range lands, and hence are the basis of animal industry. Grasses are also used in the industrial arts: sugar from sugar cane, fibers from many different species, oil from corn grains, a great variety of building materials from the bamboos, brooms from broom corn, starch and alcohol from various cereals, etc. We use grasses as soil-binding plants; to make lawns and golf courses; and many species, the plume grasses, are garden ornamentals. Truly, the grasses are indispensable to the welfare and happiness of the human race.

Is it any wonder that man has been interested in plants since the dawn of history? Primitive man soon learned that, with care, certain of the wild plants would more bountifully supply his wants. He collected seeds and planted them in crudely prepared soil; he propagated other plants by means of tubers and roots; and thus gradually he brought about the domestication of a few plants which were useful to him. He had a special interest in those plants which had real or imagined curative properties. In fact, among the earliest records of the study of plants are those which are concerned with medicinal plants.

There is a long list of medicinal or drug plants of which one may gain knowledge by examining a large volume, the *Pharmacopoeia of the United States*. The medicinal properties of many plants are doubtful and their use uncertain. There are many plant drugs with essentially the same physiological action; and a large majority of these could be discarded with no detriment to mankind. Today, many drugs are synthetically prepared, and thus our dependence upon plants as a source of drugs is not so great as formerly. Among the truly great drug plants of the world are the following: poppy (*Papaver somniferum*), which yields opium; cinchona (*Cinchona* species), the bark of which furnishes quinine; digitalis (*Digitalis purpurea*), the leaves of which

produce a glucoside, digitalin, a specific heart stimulant; belladonna (*Atropa belladonna*), from the leaves and root of which is derived atropine; and chaulmoogra (*Taraktogenos kurzii*), the seeds of which supply an oil used in the treatment of leprosy.

Man's knowledge of plants progressed slowly; it is only within the last two hundred years that we have learned something of the internal structure and the functions of plants. This field of knowledge had to wait upon advancement in other fields of science, especially the fundamental sciences, physics and chemistry. Thus, not until the magnifying lens and microscope were invented was man able to make much progress in the study of the structure of plants.

The first serious, recorded attempt to classify plants was made by Theophrastus, a Greek philosopher who lived between 370 and 285 B.C., and who was a student of both Plato and Aristotle. From his time until now, not only have hundreds of thousands of different kinds of plants been discovered in different parts of the world, and named and described, but also great improvement has been made in their classification. Today, a vast assemblage of plants, numbering approximately 250,000 species, or kinds, have been named and classified, but doubtless many species still await discovery. There are, in the various botanical publications of the world, accurate and detailed descriptions of every known species of plant. Type specimens upon which the original descriptions were based are carefully preserved in great collections called herbaria. That division of botany which has to do with the naming, description, and classification of plants is called **systematic botany or taxonomy.**

It is of great importance to understand how plants secure from the soil and air the materials essential for their growth, how these materials are transported within the plant and where they are utilized, how water is lost from the plant, and how the plant grows and reproduces—in short, it is necessary to understand the various processes or activities which are necessary to maintain the life of the individual plant and to assure the survival of the species to which it belongs. This study of the activities of plants is a special field called **plant physiology.** Improvements in methods of propagating economic plants, of cultivating and harvesting them, and of handling and storing them have resulted from physiological investigations. Plant physiology has an intimate relation to all the agricultural sciences.

If one is to understand clearly how roots absorb water and mineral salts from the soil and pass them on to the organs of the plant, it is essential to know the structure of the root; similarly, a proper understanding of reproduction by flowers must be based upon a knowledge of flower structure. That field of botany which has to do with the structure of roots, flowers, and all the other organs of plants is known as **plant morphology.**

Plants occur everywhere on or near the surface of our planet. Wherever man has gone, even in the polar regions and on the summits of the highest mountains, plants are found. Besides the familiar trees, shrubs, and herbs, there are countless small and inconspicuous plants, many microscopic, which occur in the waters of the earth, to considerable depths in the soil, and in the air. Many kinds of bacteria and other simple plants live on and within the bodies of larger plants and of animals. The thousands of different kinds (species) which make up the vast population of plants fall into different groups, each of which has certain distinguishing characteristics. The principal groups are as shown in the following table:

A Classification of the Plant Kingdom

Scientific Names of the Groups	Common Names
THALLOPHYTA	
Algae. Thallophyta which possess chlorophyll.	
Myxophyceae	Blue-green Algae
Chlorophyceae	Green Algae
Phaeophyceae	Brown Algae
Rhodophyceae	Red Algae
Fungi. Thallophyta which do not possess chlorophyll.	
Schizomycetes	Bacteria
Myxomycetes	Slime Fungi
Phycomycetes	Algal Fungi
Ascomycetes	Sac Fungi
Basidiomycetes	Club Fungi
EMBRYOPHYTA	
Bryophyta. Mosses and related plants.	
Hepaticae	Liverworts
Musci	Mosses
Pteridophyta. Ferns and related plants.	
Lycopodineae	Club mosses and related plants
Equisetineae	Horsetails
Filicineae	Ferns

Spermatophyta. Seed-bearing plants.

Gymnospermae	Conifers and related plants
Angiospermae	Flowering plants
Dicotyledones	Dicotyledons
Monocotyledones	Monocotyledons

The first part of this book is concerned with the flowering plants—their structure and their life processes. The second part deals with the great groups of plants, starting with those of simplest structure and proceeding to the more complex. It includes a description of the morphology, physiology, and relationships of the pond scums and seaweeds, of the bacteria, molds, mildews, rusts, smuts, and mushrooms, of the liverworts and mosses, of the ferns and their allies, and of the conifers and flowering plants. Such a general view of the plant kingdom is as essential to a liberal education as the study of philosophy, history, or literature. It can greatly enhance our appreciation of nature by contributing to our understanding of the world about us. It is, of course, prerequisite to more intensive study of such special fields of plant science as plant physiology, plant anatomy, cytology, genetics, and bacteriology, and of those important phases of applied botany (forestry, plant breeding, plant pathology, agronomy, and horticulture) which play so large a part in scientific agriculture.

CHAPTER II

THE PLANT BODY

The Individual Plant.—The plant kingdom is made up of a great number and almost infinite variety of plants. Over a quarter of a million different kinds, or species, have been described and named, and doubtless many remain still undiscovered and unnamed. Within any given species, there is great variation among the innumerable individuals. It is literally true that no two plants are alike. Each individual plant—whether it be a single wheat plant among millions in a field, or a single bacterium among countless others in the soil, or a single tree among its many neighbors in a forest—is a distinct and individual organism which is able to carry on all the processes necessary to maintain its life and perpetuate the species. It has a parent or parents, and a long line of ancestors behind it.

The individual plant must carry on the different processes necessary to maintain its life, must frequently undergo unfavorable environmental conditions such as water shortage and extremes of temperature, must compete with neighboring plants for light and space in which to grow, must often be subjected to the attacks of insects or other parasites, and, finally, must produce offspring.

Organs and Tissues.—We speak of the human body as being made up of a number of organs, each with certain work to do. There are organs of sight, organs of hearing, of digestion, etc. Just so we may speak of the plant body. It, too, is composed of various organs, with which it carries on its different activities. An organ is a part or member of the plant with a particular kind of work to do. For example, the roots are absorbing and anchoring organs; the stems, conducting and supporting organs; the leaves, food-making and "water-losing" organs; and the flowers are reproductive organs. If we study the structure of organs with a microscope we find that

they are composed of many small compartments or chambers, the walls of which are usually thin and transparent. Each of these microscopic chambers, with the living substance which it contains, and which will be discussed in the next chapter, is called a **cell.** Just as a honeycomb is made up of separate units or compartments, so is the plant body made of separate units, the cells. It is in the cells that all the complex physical and chemical changes of the living body take place. Cells of similar structure which together perform a special function constitute a **tissue.** Thus such an organ as the leaf is composed of several different kinds of tissues, including, in this case, conducting tissues, protective tissues, and food-making tissues.

Some plants consist of but a single cell, and others have but few distinct organs, or a few tissues, with which to carry on the different functions. Such plants are said to be simply organized. Examples are the pond scums, seaweeds, molds, mildews, rusts, smuts, etc. Many plants have numerous distinct organs and many tissues with which to carry on the separate functions. This is true of the more familiar plants of orchard, garden, field, and forest. Such plants are said to be highly organized.

If we consider the various activities or functions of a plant body, we find that they fall into two groups: **vegetative** and **reproductive. Vegetative activities** are those which have to do with the growth and preservation of the individual. In seed plants they are carried on by the roots, stems, and leaves. The principal vegetative activities or functions of the plant are **absorption** of raw materials (water, carbon dioxide, and inorganic salts) from the soil and atmosphere; **transfer** (movement) of raw materials and of food (mostly made in the leaves) within the plant body; **manufacture of foods** (carbohydrates, fats, and proteins); **assimilation** (the process by which foods are transformed into the living material—protoplasm); **respiration** (a "breaking down" of substances in the cell, which provides energy for the work of the plant and in which oxygen is taken in and carbon dioxide given off); and **transpiration** (water loss). **Reproductive activities** or functions are those which have to do with the preservation of the species to which the individual belongs. In seed plants these activities are associated with the flower parts, fruits, and seeds.

It is possible for the grower to control somewhat the vegetative and reproductive activities of plants. Certain plants, such as spinach and lettuce, are grown for their leaves, structures having to do solely with vegetative activities. On the other hand, many plants are grown for their flowers, fruits, and seeds, structures concerned with reproduction. If the plant is well supplied with nitrogen, such that in its tissues there is a carbohydrate content relatively low in proportion to the nitrogen content, the plant will tend to be vegetative and the initiation of flowering and fruiting will be retarded. On the other hand, if the plant grows under conditions which limit the supply of nitrogen moving into the plant from the soil, such that the nitrogen content of plant tissues is relatively low in proportion to their carbohydrate content, the plant will tend to be reproductive.

Kinds of Plant Bodies.—We are familiar with the very wide variation in the form of the animal body in the animal kingdom. If we take into consideration the microscopic animals of water and land, the vast assemblages of insects, crustaceans, worms, vertebrates, and other groups of animals, almost every conceivable form of animal body would seem to be represented. In most cases, the form of the body is fairly well adapted to the environment and mode of living of the organism. If it were not, the organism would not be likely to survive and produce progeny. It is obvious that fish have a form and structure of body which adapt them to life in the water; and birds, a form suited to free and rapid movement in the air.

Likewise, in the plant kingdom there is a great variety in the form of the plant body, and these forms are usually well adapted to the environment and the manner of living of the plant. The mention of a few common plants may call to mind some of the different forms of the plant body: seaweeds, bread mold, wheat smut, mushrooms, mosses, ferns, and the great variety of herbs, shrubs, and trees.

The simplest kind of plant body is found in those species in which the whole plant consists of a single cell. Among such simple unicellular (one-celled) plants are the bacteria and certain algae. One common unicellular alga is *Protococcus*. Great numbers of these plants make up the green growth often found (in the northern hemisphere) on the north side of tree trunks, fence posts, and walls. A plant body in which similar cells are joined end to end to form a thread or filament represents an advance in complexity over the unicellular forms. There are many thread-like or filamentous algae,

such as *Spirogyra,* one of the pond scums; also many filamentous fungi. If all the cells of such a group are alike both in structure and in their activities and are able to carry on their normal life function even if they are separated from the group, we speak of them as **colonial forms.** In certain filamentous algae, *Oedogonium,* for instance, there is a slight degree of specialization among the cells in the filament, in that some cells are different in structure and function from the rest and perform certain work for the whole group. Such plants are truly **multicellular.** In some of the seaweeds (*Ulva,* or sea-lettuce, for example) the plant body is a flat plate, two cells thick. In other more complex seaweeds and in such fungi as the mushrooms there is a rather complex and extensive plant body with several tissues adapted for different functions, but in none of the fungi or algae are there true stems or leaves. Thus, there are plant bodies consisting of but one cell (unicellular plants); others, of chains of cells, or of plates of cells all alike (colonial forms), or with slight differentiation among the cells (simple multicellular plants); and still others composed of innumerable cells making a plant body of the form with which we are most familiar.

The Plant Body of Seed Plants.—The most common and the best-known plants in the world are seed plants. In plants of this type the body is essentially a more or less lengthened axis, made up of two principal parts, the **shoot** (usually above ground) and the **root** (usually below ground). Both the shoot and the root are generally branched, and their branches may in turn branch repeatedly. The shoot consists of two principal organs, **stems** and **leaves.** The most conspicuous kinds of leaves are the green foliage leaves and those which compose the parts of the flower (floral leaves). Smaller and less conspicuous are the leaves which form bracts or bud scales.

There are certain marked differences between the stem and root. The most obvious is the division of the stem into joints or sections, with branches or buds, which are rudimentary branches, arising at regular intervals, whereas roots do not have such joints or sections, but branch irregularly. The slightly enlarged portions of the stem where leaves and buds arise and branches originate are called **nodes.** The portions of the stem between successive nodes are **internodes.** They are generally much longer than the nodes. Roots are not

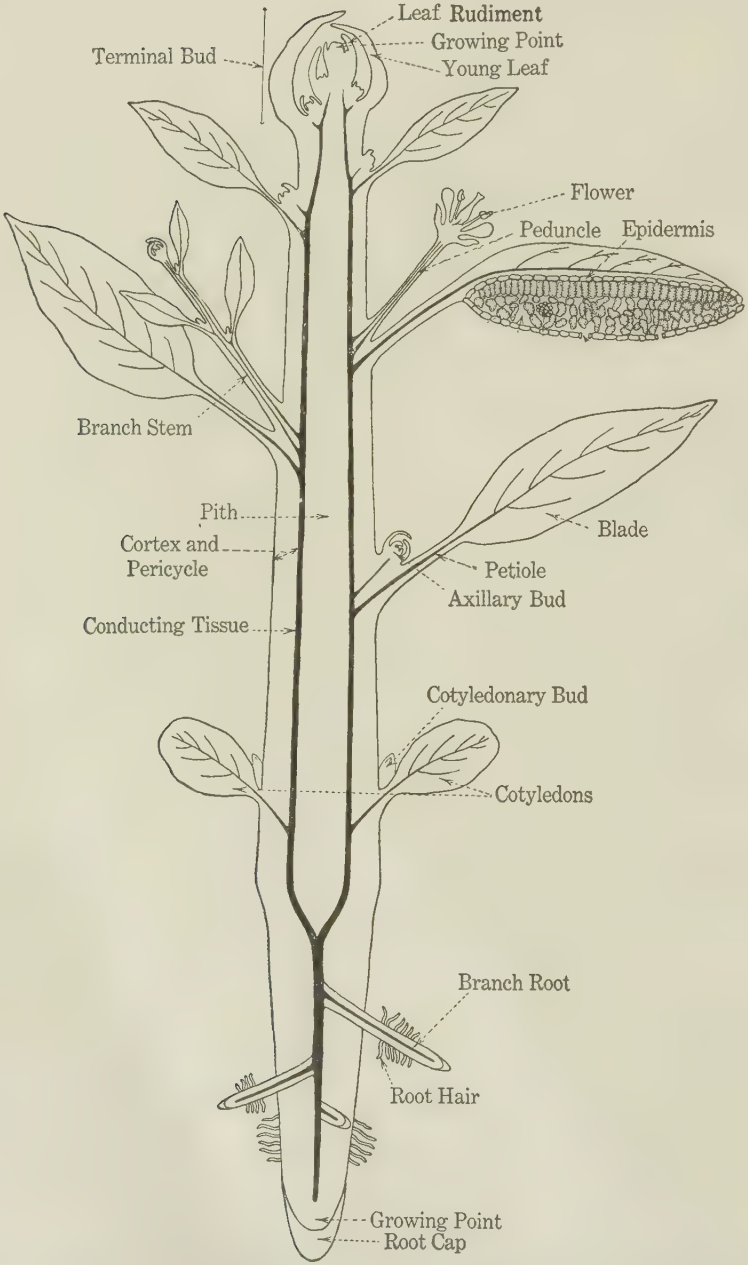


FIG. 1. Diagram showing the principal organs and tissues of a typical seed plant. (Modified after Sachs.)

divided into nodes and internodes. There are other differences between the stem and root which will be discussed later.

Functions of Stem, Root, and Leaf.—The principal functions of the stem are (1) the support of the foliage leaves and flowers in positions favorable to the performance of their functions; (2) the conduction of raw materials (water and mineral salts) from the roots which absorb them from the soil; and (3) the conduction of plant foods (for example, sugars, fats, and proteins) from the places where they are manufactured, to points where they are needed for growth or other processes, or where they will be stored for future use.

In addition to these principal functions, stems may perform several other less important functions. Green stems supplement the leaves in food manufacture. In some plants, stems act as storage organs, of starch, for example, in the underground stems (tubers) of the potato, of sugar in the sugar cane, and of water in cacti; or as organs of vegetative reproduction, as do the tubers of the potato, the bulbs (short stems with fleshy scale-like leaf bases) of the onion, the runners (creeping stems) of the strawberry, the rhizomes (underground stems) of the wild morning glory, etc.

The principal functions of the root are (1) anchorage, and (2) absorption of raw materials (water and certain mineral salts) from the soil. A secondary function is food storage. Common examples of roots which act as storage organs are those of sugar beet, turnip, and sweet potato.

The principal functions of the leaf are the manufacture of sugar and starch (carbohydrates), a process known as photosynthesis, the synthesis of nitrogenous foods, and the giving off of water in the form of water vapor, a process called transpiration.

General External Features of the Shoot.—We may classify the shoots of most plants as erect, prostrate or climbing. The shoots of most plants grow erect, but the shoots of such plants as the cucumber, squash, watermelon, and strawberry are prostrate on the ground. Plants which climb upon other plants and depend upon them for mechanical support, that is, plants with climbing shoots, are known as lianas. Examples of lianas are the scarlet runner bean, dodder, hop and grape.

There are two principal forms of erect shoots—excurrent and

deliquescent. Such plants as the pines, spruces, and firs generally have a single main stem with many lateral branches. So also in the Carolina poplar there is a "leader"—one main stem which generally continues to be the principal stem throughout the life of the plant. This type of shoot is said to be **excurrent.** In the oak, common cottonwood, apple, and many other kinds of trees, the principal stem

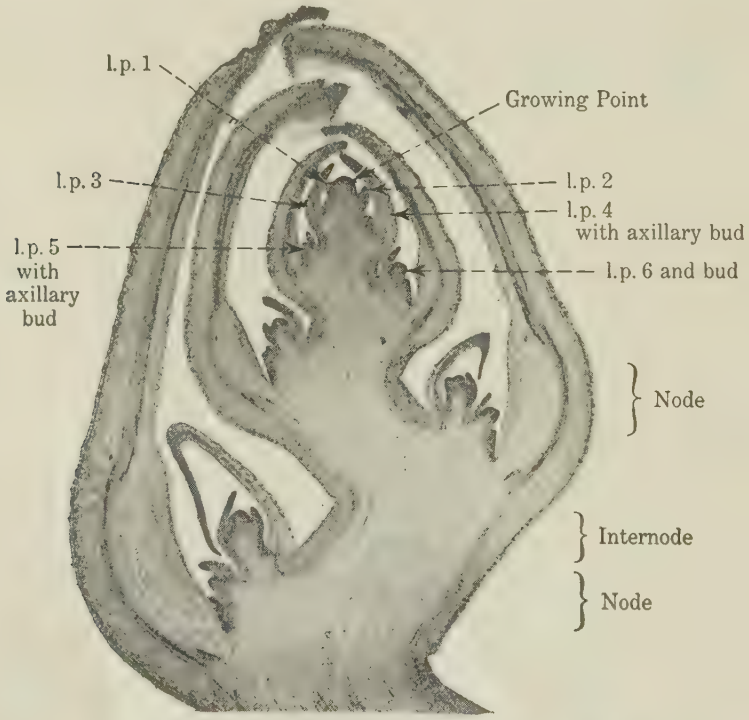


FIG. 2. Photomicrograph of a leaf bud of Dutchman's Pipe (*Aristolochia*) in longitudinal section showing the growing point, the leaf primordia (numbered in the reverse order of their formation), and rudimentary lateral buds in the axils of the older leaf primordia.

does not continue through to the top of the tree but is replaced above by several large branches so that it is impossible to distinguish any one main stem except at the base of the tree. Such shoots are spoken of as **deliquescent.**

Buds.—The characteristics of buds are best seen in woody plants. If we examine an ordinary bud of any common woody plant, we find that it is made up of a mass of very tender tissue surrounded

by overlapping scales. The bud is, in fact, a short length of partially developed stem with very short internodes and with rudimentary leaves in various stages of development, the whole protected by the bud scales which enclose it. That the bud is actually a shoot becomes clear when we cut the bud lengthwise and study its structure with the aid of the microscope (Fig. 2). It is also shown by the fact that branches always develop from buds. For example, we are familiar with the common horticultural practice of bud grafting, in which buds are removed from the stems on which they originated and with certain precautions set into the stems of other plants where they subsequently develop into branches.

The most important feature of a bud is the delicate growing point, that is, the extreme tip of the stem within the bud, with the rudimentary leaves which arise from the growing point and surround it. In trees and shrubs of cold and arid regions, these tender structures, the growing point and the rudimentary leaves, are usually protected by several layers of overlapping bud scales, which are in reality modified leaves. These bud scales may be covered with hairs, as in the willow, or with a resinous secretion, as in the cottonwood. These coverings very effectively protect the delicate parts within from drying out, as well as from mechanical injury. Contrary to the usual opinion, bud scales do not protect the delicate structures within from freezing; actual measurements show that temperature on the inside of a bud is little, if any, higher than that outside. Naked buds are not protected by scales. Such naked buds are characteristic of the woody plants of the moist tropics, and of non-woody (herbaceous) plants the world over.

The Position of Buds on the Stem.—As to their position on the stem, buds may be classified as (1) terminal, (2) axillary, or (3) adventitious. Generally, every stem ends in a bud which is, therefore, called a terminal bud. As a rule, the terminal bud is the most vigorous of all the buds on the branch, for the part of the stem which develops in a single season from the terminal bud is longer than any of the branches which develop from other buds on the same stem.

Moreover, in many herbaceous and woody plants, the terminal bud often exerts an inhibiting influence upon the development of lateral buds, exhibiting what is termed apical dominance. By

this is meant that, as long as the terminal bud is vigorous and active, the lateral buds in the axils of the leaves on the same stem do not develop into branches; but, if the terminal bud is injured or removed, one or more of the lateral buds at once become active. There is evidence that apical dominance is due to the presence of the hormone, auxin, in the apical bud.

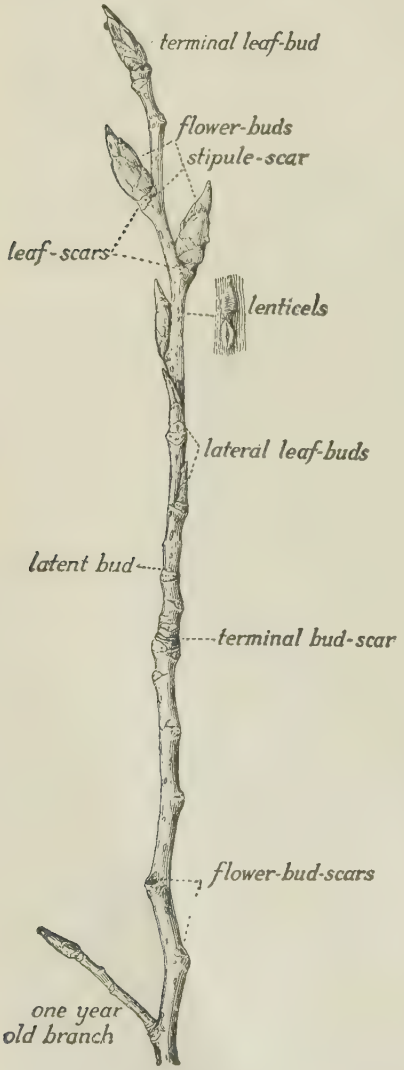


FIG. 3. Twig of cottonwood (a species of *Populus*) showing two years' growth. (From Robbins' *Botany of Crop Plants*, after Longyear.)

Axillary buds are buds which arise in leaf axils (Latin, *axilla*, little armpit), that is, just above the place on the stem where a leaf is attached. They may give rise to leafy branches, to flowers, or to both. On very short branches, such as the fruit spurs of apple and cherry trees, it is sometimes difficult to distinguish between the terminal and axillary buds. Accessory buds are extra buds developed in the leaf axil in addition to the single axillary bud regularly occurring there. Such accessory buds are found, for example, in the maples and box elders.

Axillary buds may be classified as to the number at a node into: (*a*) **alternate**, (*b*) **opposite**, and (*c*) **whorled**. When one bud occurs at each node, as in the apple, peach, plum, and cottonwood, they are said to be **alternate**. When there are two buds at a node, on opposite sides of the stem, as in the mints, box elder, and maples, they are **opposite**.

When more than two buds occur distributed around the stem at each node, as in catalpa, they are said to be whorled. In the relatively rare cases where the single principal bud at each node is accompanied by one or more accessory buds arising near the base of the principal bud the leaf arrangement is spoken of as alternate, not whorled.

Adventitious buds are buds which arise anywhere on the plant except at the tip of the stem or in the axils of leaves. They may arise on stems or roots, or even, very rarely, on leaves. Their formation is usually stimulated by injury. For example, when a branch is cut back, as in pruning, numerous adventitious buds may arise at the edges of the cut surface.

Adventitious buds may be induced to grow by employing growth substances. For example, it has been shown that when cuttings of the Rose of Sharon, with all the normal buds cut away, were exposed to vapors of certain growth substances, they developed a large number of adventitious buds, especially on the upper portions of the cuttings.

Dormant buds are ones that have arisen in a regular fashion in the leaf axil, but which, for some reason, have not developed. In woody plants which live for many years, such buds may lengthen somewhat each year so that the growing point remains at the surface of the bark. Such buds may renew their activity later in the life of the plant, being forced into growth by some stimulation, such as severe pruning of parts above.

The Contents of Buds.—Classified as to the structures which they contain, buds are (1) leaf buds, (2) flower or fruit buds, or (3) mixed buds. When a leaf bud is cut open it is found to contain a growing point and a much shortened axis or rudimentary stem bearing a number of small leaves; since by elongation it may develop into a leafy branch, an axillary leaf bud may be as properly called a branch bud. The new branch stem, like the old branch from which it came, has buds in the axils of its leaves and itself ends in a terminal bud.

A flower or fruit bud is one containing flower parts but no foliage leaves. If we open a bud of this type, we find one or more young unexpanded flowers. In cherries, for example, the number of flowers in a bud varies from one to five. A cherry bud having five flowers may develop a cluster of five cherries if nothing inter-

feres with the development of a fruit from each flower. Flower or fruit buds are sometimes terminal, as in the loquat, but are commonly axillary, as in the peach, cherry, and walnut.

A mixed bud is one that contains both flowers and leaves. When a bud of this type unfolds there is produced a leafy shoot which either (*a*) terminates in a flower cluster, or (*b*) bears flowers or flower clusters in the leaf axils. The first-mentioned type of mixed bud is characteristic of the apple, pear, blackberry, grape, and many other plants; whereas the second type is found in the persimmon, mulberry, fig, oak, and a number of others.

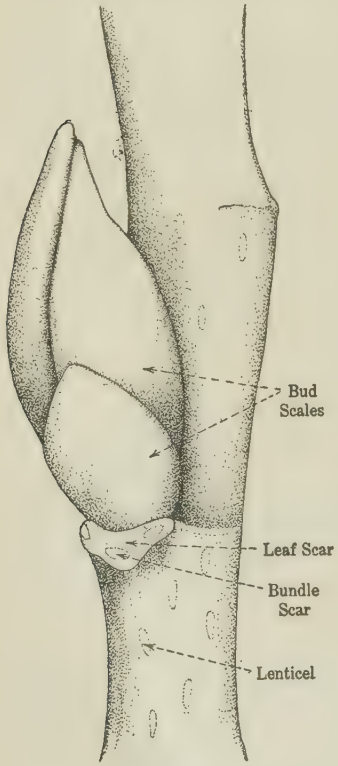


FIG. 4. External view of a portion of a stem of cottonwood (a species of *Populus*) showing an axillary leaf bud, leaf scar and lenticels.

It is not always possible to distinguish leaf buds by their external appearance from buds which will produce flowers. In some cases, however, they have a different shape. In the apple, for example, the buds which produce flowers (here, really mixed buds) are rather thick and rounded, whereas leaf buds are smaller and more pointed. In all plums the flower buds are lateral, and usually stand out at an angle of about 30°, whereas leaf buds lie closer to the stem.

The axillary buds generally decrease in activity with their distance from the terminal bud. Buds several internodes distant from the apex of the stem are generally dormant and normally do not develop at all into branches. In most plants the removal of a terminal bud or of the upper end of a branch increases the activity of the axillary buds below the cut end, and as a result some of these buds, which would otherwise have remained dormant, may become active.

Many buds which are apparently adventitious are often in reality

axillary buds which have remained dormant so long that their original position relative to a leaf, long since shed, is difficult to ascertain.

Branching.—The branching system of the shoot is determined largely by the arrangement of the buds. Plants with alternate buds have alternate branches also, but the branches are much less con-

FIG. 5. Three twigs of ash (*Fraxinus*) showing the opening of the terminal bud. The bud to the left is swelling but the bud scales have not yet separated. The bud scales of the second bud have separated but as yet the internodes and rudimentary leaves within the bud have grown very little. The picture to the right shows the bud fully opened and leaves and internodes well advanced in development.

stant and regular in their alternate arrangement than are the buds. Many buds remain dormant, and of the active buds some die because of the attacks of insects or disease, or for other reasons, and do not produce branches.

It is a common and well-known practice of orchardists and gardeners to change the form of plants while they are still young by pruning, which is the judicious removal of buds or branches. The removal of terminal buds or terminal portions of branches will stimulate the development of axillary buds, cause a spreading of

the plant, and thus produce a broad tree with a "low head." A cylindrical or pyramidal type of tree may be secured by removal of a certain number of lateral buds or branches.

The Stems of Woody Deciduous Plants in Their Winter Condition.—A several-year-old twig of such a plant is illustrated in Fig. 3. At the tip is the large terminal bud, and at each node there is an axillary bud. Below each axillary bud is a semicircular or

FIG. 6. Five twigs of buckeye (*Aesculus*) showing successive stages in the opening of the terminal bud and in the growth of the internodes and leaves which, in a rudimentary condition, were contained within the bud. All the parts above the dotted line belonged to the terminal bud or were developed within a period of three weeks from a terminal bud like the one shown at the extreme left. The scale at the bottom of the figure is a decimeter scale.

elliptical **leaf scar** which was left when the leaf, in the axil of which the bud was formed, became detached from the twig. When a woody plant is in the leafless condition, the number of these scars at a node shows whether the leaf arrangement was alternate, opposite, or whorled.

The end of the growth in length taking place each year is marked by the ring of **bud-scale scars** left when the close-set bud scales of the terminal bud are shed in the following spring. The spacing of these

rings often reveals striking differences in the amount of growth produced each year, for there is practically no increase or decrease in the length of any portion of a stem after that portion is a year old.

On some twigs, flower-bud scars may also be found where the short branch which developed from a flower bud became detached from the stem after the fruit had matured.

Close examination of the surface of the twigs where there are none of these various kinds of scars will reveal numerous lighter-colored, slightly raised spots on the bark. These **lenticels** are particularly conspicuous in the cherry, birch, and elderberry. They consist of porous tissue which permits the passage of gases inward and outward. Except for these lenticels, the bark would almost completely prevent the movement of air into or out of the stem.

In the identification of woody plants, the trees and shrubs, it is usually considered necessary to make use of leaf, flower, and fruit characters. However, by a careful study of buds and twigs it is possible to identify our trees and shrubs in their winter condition.

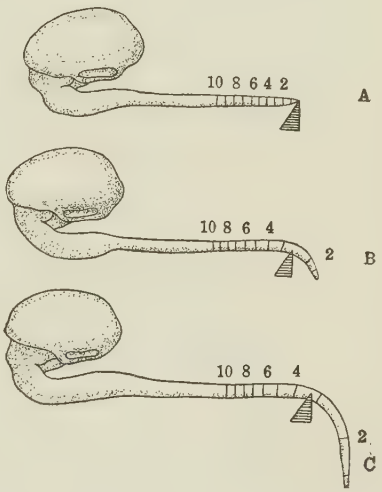


FIG. 7. A seedling of white lupine (*Lupinus albus*) at the time it was placed in the horizontal position (*A*), and after a shorter and longer period (*B* and *C*) in the new position. The end of the root is marked off into zones beginning with the extreme tip of the root and each originally one millimeter long. Note that the region of curvature corresponds with the region of most rapid elongation and that the sensitive region (included in the first two millimeters) does not elongate much during the curvature. (Redrawn from Sachs.)

Factors Which Determine the Direction of Growth of Different Parts of the Plant Body.—*Geotropism.*—In most plants the main stem tends to grow vertically upward, and when there is a single primary or tap root that root tends to grow vertically downward. On level ground the direction of growth of the main stem and root is thus generally at right angles to the surface. On a slope, however, it is clear that the stem is not at right angles to the surface of the soil but that it tends to be truly perpendicular, that is, follows

the direction of the earth's radius passing through the base of the stem. Regardless of the slope of the land, the tap root also tends to grow perpendicularly, but in the opposite direction from the main stem.

When a seedling, or an older plant having a single primary root and one main stem, is placed in a horizontal position, the growing region of the root will bend until it points downward and the growing portion of the stem will curve upward. This orientation of stem

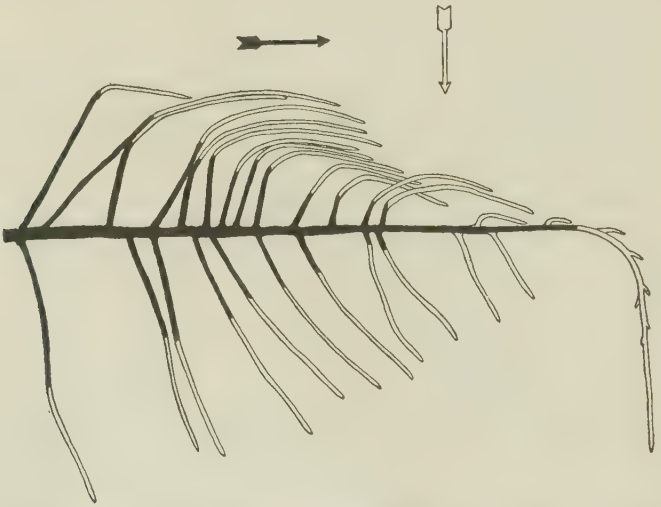


FIG. 8. Diagram of the root system of the broad bean (*Vicia faba*) showing the orientation of the secondary roots as contrasted with the orientation of the primary root. Originally the whole primary root was growing parallel to the direction of gravity, shown by the solid black arrow. Then the root system was turned through 90° so that it was at right angles to the direction of gravity (outlined arrow). Growth of the root system before and after the change of position is indicated respectively by solid black and outline portions of the figure.

and root is a response to gravity and is called **geotropism** (Greek, *gē*, earth, + *tropos*, turning). It is a very remarkable fact that when a plant is displaced from its normal position the main root and the main stem react to the same stimulus with exactly opposite reactions. Organs which, like the main root, bend downward when displaced from their normal position are said to be **positively geotropic**; those which bend upward are spoken of as **negatively geotropic.**

Geotropism is one of the most important of the several different

tropisms met with in plants. All these tropisms have the following characteristics in common: (1) The reaction is always a curvature resulting from more active elongation on one side of the organ than on the other; (2) the stimulus (gravity, light, etc.) must not act equally in all directions but must be a "one-sided" stimulus; and (3) the curvature ceases when the organ has reached a certain definite position relative to the direction of the stimulus.

An illustration of the advantage of geotropism to plants is the recovery of the normal erect position by grain which was "lodged" because of heavy rains or high wind. Such lodged grain is at first prostrate on the ground or semi-prostrate. If the plants are not too old, geotropic curvature takes place at the nodes, and the upper parts of the plants are thus again brought into the normal, perpendicular position. In wheat, oats, barley, and other grains the stem is surrounded, just above each node, by a thick cushion of tissue which is really part of a leaf base. As long as the stem remains perpendicular this tissue does not grow. However, when the stem is placed in a horizontal position or is much removed from the perpendicular, the tissue of the underside of this cushion is stimulated by gravity to renewed growth so that the stem is bent upward at that place and the upper side of the cushion somewhat compressed. If several such cushions react thus, the upper part of the shoot may be brought into the normal position. It is an interesting fact that if the stem is rotated around a horizontal axis at a constant speed the whole cushion of tissue responds to the stimulus of gravity by growing on all sides, and the stem, instead of bending, will increase considerably in length.

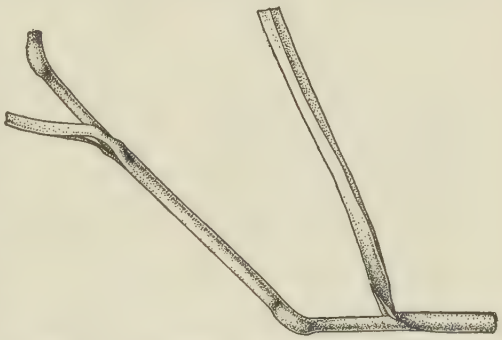


FIG. 9. A "lodged" grass stem showing the upward bending at the node resulting from the geotropic reaction of the cushion of tissue around the node.

Phototropism.—If a house plant is placed at some distance from a window, the growing part of the stem will tend to curve toward the window. Actually it will not grow directly toward the light because

geotropism will tend to keep it growing perpendicularly upward. The direction in which it grows will be the resultant of two tendencies: (1) the tendency to grow parallel to the direction of gravity, and (2) the tendency to grow parallel to the direction of the illumination. This tendency of different organs of the plant to take up a certain characteristic direction relative to the direction from which light falls upon them is called phototropism (Greek, *phōs* (*phōt-*), light, + *tropos*, turning). The main stems of most plants are **positively phototropic** (bending in the direction from which comes the most intense illumination). Only in a few plants is it possible to show that roots are at all phototropic, but in these rare cases (*Sinapis*—white mustard) they are negatively so. Leaves are commonly phototropic, the leaf stalks or petiole being able, when young, to bend until the leaf surface is not parallel but approximately at right angles to the direction from which the light comes.

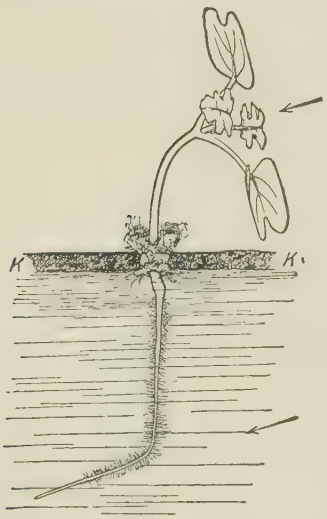


FIG. 10. Mustard seedling growing in water showing the positively phototropic curvature of the hypocotyl and the negatively phototropic curvature of the root. The arrows show the direction from which light is falling upon the plant. (After Noll.)

Other Tropisms.—Many other factors of less importance than gravity and light may cause similar curvatures when they do not act equally on all sides of an organ. Some of these factors are (1) differences in the quantity of moisture in the medium surrounding the organ in question, (2) differences in the concentration of certain other substances in the medium, (3) differences in temperature in the medium, (4) contact of one side of the plant organ with some solid object (curvature of tendrils), etc.

In the various kinds of tropisms which occur in plants the actual bending of the organ is the result of more rapid elongation (growth) on the side of the stem, root, tendril, or other organ which becomes the convex side of the organ after it bends. A tropism is never the mere passive curvature of an organ under its own weight, such as

occurs when a long piece of wire or a slender branch, whether dead or alive, is placed in a horizontal position and held by one end only. In a tropism a "one-sided" external stimulus is responsible for the occurrence as well as the direction of the curvature, but the plant itself curves by reason of a different rate of growth on the two sides of the organ. Accordingly, the curvature of roots generally takes place near the tip; of stems, throughout the region of elongation.

The question now arises: What causes a difference in the rate of growth on the two sides of the organ? It has been demonstrated that growth hormones play an important rôle in this phenomenon. In stems growth hormones must be present in the growing regions in order that the enlargement of the cells shall occur. When the shoot, for example, is illuminated from one side, these growth hormones accumulate on the shaded side of the stem tip, move down the stem, and stimulate a greater elongation of the cells on the shaded side than of those on the illuminated side. As a result the stem bends toward the light. Or, as another example, if a shoot is placed horizontally, then growth hormones accumulate on the under side of the stem tip, thus stimulating a greater enlargement of the cells there than on the upper side, with the result that the stem tip bends upward. Peculiarly, roots react to these hormones differently from stems; they retard rather than accelerate the enlargement of root cells. For example, when a root tip is placed horizontally, as in Fig. 8, the growth hormones accumulate on the lower side of the organ, thereby retarding rate of growth of the cells on that side; and as a result the root tip bends downward.

Nastic Curvatures.—Curvatures of another type, also caused by external stimuli but quite distinct from tropisms, are the so-called nastic curvatures. The most familiar examples of such curvatures are those which bring about the opening of various flowers when they are illuminated. The petals curve outward when light falls upon the flower. These curvatures differ from tropisms (1) because the stimulus need not be "one-sided" (the flower, for example, opens even though it is illuminated equally from all sides), and (2) because the direction of the curvature (outward from the center of the flower) is not affected by the direction of the stimulus. Various external stimuli may produce nastic curvatures.

The Life Cycle.—Every plant, like every animal, begins its life as a single cell. In very simple plants, such as the bacteria and certain blue-green algae, this single cell is the individual plant itself. When it divides, the cells separate and two new individual one-celled plants are formed; these in turn grow and divide, and so on. The life cycle of such a plant is short and simple. In higher plants, such as wheat, the beet, and the apple, the life cycle is much more complex and of longer duration. According to their length of life, plants may be classified as annuals, biennials, and perennials.

An annual is a plant which completes its life cycle within one year's time. In wheat, for example, the seed germinates, roots and leaves are produced, and in one season the plant reaches adult size. After this relatively brief period of vegetative activity, flowers and seeds are produced, and within every seed there develops a rudimentary wheat plant, the embryo of the seed. The parent plant then dies. Thus the life cycle of this annual plant is completed within a single year. In cool climates certain plants behave as winter annuals. In these cases the seeds germinate in late summer or fall, the young plants live throughout the winter, and in the following spring they send up flower stalks, blossom, and bear seed. Most annual plants propagate themselves entirely by seed. Consequently, all methods of combating the common annual weeds, such as wild oats, mustard, shepherd's purse, lamb's quarters, and Russian thistle, are directed at the prevention of seed production.

A biennial is a plant which completes its life cycle within two years and then dies. The beet plant may be taken as a type of biennial plant. The embryo plant resumes its growth at the germination of the seed, and during the first season produces a number of large leaves crowning a fleshy root, the "beet." In contrast with the annuals, no flowers and seeds are produced the first year; instead the plant is engaged chiefly in storing food in the root. In the fall the leaves die, but the "beet" (root) remains alive, except in regions of severe winters where it must be dug and stored to protect it from freezing. The next season the "beet" sends up a shoot 3 to 4 feet high, which gives rise to flowering branches. The flowers produce seeds, and soon afterward the plant dies. As in the case of the wheat plant, the beet plant has but one period of seed production, after which the whole plant dies, but the beet, like all other biennials,

requires two vegetative seasons to complete its cycle, whereas the wheat plant requires but one year. Like annuals, biennials propagate themselves solely by seed. Common biennial weeds, such as wild carrot, wild parsnip, mullein, and bull thistle, are effectively held in control by the prevention of seeding.

All the familiar trees and shrubs are good examples of plants which live more than two years. Thus in the apple, after seed germination a succession of growth periods occurs during which there is no production of flowers and seed, but at the age of four or five years flowers and seed are produced. From this time on the tree continues vegetative activities for many years and each year produces flowers, fruits, and seeds. Such plants are said to be **perennials.**

The most troublesome weeds are perennials, for they cannot be destroyed by merely preventing their seeding. Furthermore, many perennial weeds are able to produce new plants from fragments of their roots (dandelion) or underground stems (quack grass, wild morning-glory, etc.). Accordingly, attempts to destroy these weeds by digging them up may increase rather than decrease their number.

We see from the above discussion that in plants there is a cyclical periodicity of vegetative and reproductive activities. In annuals and biennials, the period during which vegetative organs are formed necessarily precedes that during which reproductive organs are produced. After seed production, all organs of the plant die except the seeds. However, the ordinary life cycle of annuals and biennials can be modified in various ways. For example, removal of the flowers and fruits may throw the plant back into the vegetative cycle; or certain biennials, grown under conditions which provide them with more warmth and a longer season than that to which they are accustomed, may become annuals. In temperate climates perennials manifest different types of periodicity. The reproductive period (blooming) of most perennials follows a long season of vegetative activity. Others, like apple, cherry, maple, elm, cottonwood, etc., bloom very early, before vegetative growth is resumed or during the early stages of new vegetative development; and still others, such as the mulberry, bloom during the period of maximum vegetative growth.

Attention was called above to the biennial habit of the beet. For over a hundred years nearly all the sugar-beet seed used in the United States has been imported from Central Europe. There, the roots are grown from seed the first season; then they are removed from the soil and stored in ground silos over winter; the following spring the roots are removed from the silos, and each one set out by hand in the field; and, during the second season, a flower stalk arises and seed is produced. Recently, in certain favorable sections of western United States, where the winters are mild, sugar-beet seed has been successfully grown by the "overwintering" method. In this the life cycle is shortened somewhat. Seed is planted in August or September; by the time cold weather sets in, the roots have made considerable growth; they are left with their leaf growth undisturbed in the soil during the winter. The following season seed stalks are produced and seed harvested in July. Thus is the sugar beet, normally a biennial, induced to perform as a winter annual. It is of interest to know that the young beet plants fail to produce seed stalks if the winter is too mild. Apparently the plants must be subjected to low temperatures in order to induce those physiological changes in the plant which lead to the production of flowers and seed.

There are numerous ways of modifying the life cycle of plants. The "vernalization" of seeds may be cited as one way which is of practical importance. For example, it is possible by special treatment to induce winter cereals, planted in the spring, to produce grain the same growing season. The seeds are exposed to a low temperature for nine to ten weeks before sowing, which treatment speeds up the flowering of the plants which grow from these seeds.

CHAPTER III

THE CELL

In 1590, the brothers Jansen, spectacle makers of Middleburg, Holland, invented the compound microscope, an instrument which was destined to become the most important tool of biological science. It has made possible much of the progress in our knowledge of plants and animals, particularly in medicine, in agriculture, and in the study of heredity. Robert Hooke, an Englishman who lived from 1636 to 1703, vastly improved the microscope and with great curiosity used his microscope to examine all sorts of things. Among them was ordinary bottle cork, which he saw was made up of numerous compartments resembling the cells of honeycomb. So Hooke named these units of structure **cells.** But he saw in the sections of cork tissue only the walls of the cells, and even his later observations of living plant tissue revealed no cell contents. His failure to observe any material within the living cells was due undoubtedly to imperfections of his microscope. It was not until 1772 that Corti observed a slimy, transparent substance in the cell, which we now know to have been the **protoplasm,** or living substance. About sixty years later, an Englishman, Robert Brown, first recognized the importance of a round or oval body in the protoplasm of every cell, a body which has come to be known as the **nucleus.** In 1838, the Germans Schleiden and Schwann promulgated the cell theory, which, in the words of Schwann, was as follows: "The elementary parts of all tissues are formed of cells in an analogous though very diversified manner, so that it may be asserted that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells." It was not until 1861 that Max Schultze formulated what is known as the protoplasmic doctrine, which says that the essential part of a cell, the part responsible for its life, is the **protoplasm,** and that the protoplasm of plants and of animals is essentially very similar.

The studies of plants and animals made with the aid of the compound microscope, an instrument invented 350 years ago, have profoundly modified our conceptions of living organisms. We know now that each plant or animal is an assemblage of elementary units or cells; that cells arise only by division of pre-existing cells; and

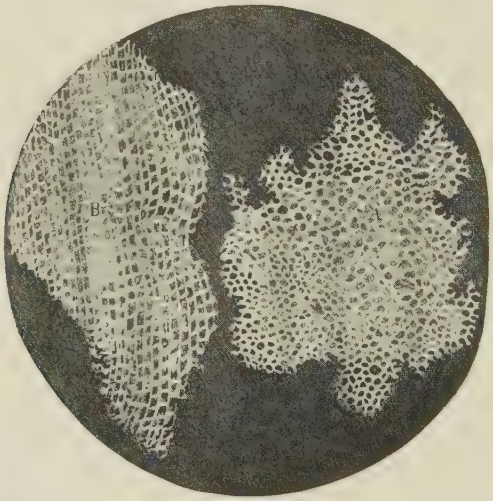


FIG. 11. Robert Hooke's illustrations of cork cells as he saw them under his microscope. Reduced facsimile reproduction from his *Micrographia* published in 1665.

that the viscous, transparent substance in the cell, the protoplasm, constitutes the physical basis of life.

STRUCTURE OF THE CELL

If we cut a thin slice from a root, stem, leaf, or any other living plant structure and examine it with a microscope, magnifying about 50 diameters, we find that it is made up of many small chambers separated from each other by walls which are generally thin and transparent. If we examine thin sections of living plant tissue, using high magnifications, we observe that within each of the compartments there is a small quantity of a viscous, almost transparent, substance. This is **protoplasm**, the living substance. The protoplasm within a single cell cavity is called a **protoplast**. Cells, each consisting of a protoplast with its surrounding wall, are the units of plant structure. Most plants are multicellular, that is, they are

composed of many cells, hundreds, thousands, or even millions of them. For example, it is estimated that there are more than fifty million cells in an apple leaf of average size. Yet every activity which the plant performs is but the expression of the activities of individual cells, and in unicellular (one-celled) plants all of the essential life processes may be carried on within a single protoplast.

The Cell Wall.—One of the most useful materials in the world is wood. From it man has constructed houses, furniture, water-craft, musical instruments, and thousands of other useful articles. Wood is composed almost wholly of the walls of cells whose protoplasm has died and dried up. The cell wall is chiefly **cellulose**, a compound belonging to the group of chemical compounds called the carbohydrates. Other familiar examples of carbohydrates are starch and the sugars.

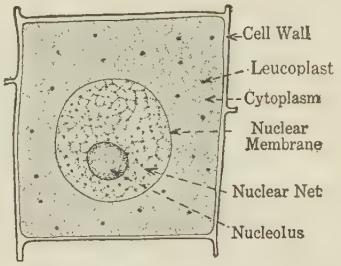


FIG. 12. A cell from the meristematic tissue of the growing point of an onion (*Allium cepa*) root.

Cellulose is destined to become one of the most valued products in the commercial world. Cotton, linen, hemp, and wood consist almost entirely of cellulose. The wood from thousands of acres of forests each year is ground up to be used in the manufacture of pulp for paper and other purposes. In the raw pulp, cellulose is in part combined with lignin, and it is necessary to separate this useless product from cellulose; this is accomplished by chemical means. Cellulose treated with nitric acid in the presence of sulphuric acid forms a cellulose nitrate, known as guncotton, which is the basis of dynamite and smokeless powder. Cellulose treated with strong acetic acid gives cellulose acetates, from which are made the non-inflammable motion-picture films. Cellulose may be converted, by digestion with dilute sulphuric acid under heat and pressure, into dextrose, which may in turn be fermented to form alcohol. Thus does wood, in fact anything of a woody, starchy, or sugary nature, become a source of fuel for motor cars and airplanes. In European countries, where gasoline is more scarce than in the United States, alcohol constitutes a sizable proportion of motor fuel. The sun's energy, captured by the chloroplastids, is indirectly utilized to drive airplanes.

The wall of the cell is secreted by the protoplast. When the cells are young, the walls are very thin, but as they grow older successive layers of cellulose are added so that the wall may finally come to

have a thickness many times as great as when it was first formed. The original thin wall separating two adjacent protoplasts is called the middle lamella. It is composed largely of colloidal pectic compounds. Certain of these easily change into pectin, a substance which causes fruit jellies to stiffen when present in sufficient quantities and accompanied by proper proportions of fruit acid and sugar.

The Protoplast.—The term protoplast is a useful designation for the mass of living material found within a single cell cavity.

Protoplasm is a semi-transparent, slime-like substance, having generally the consistency of white of egg. It is not a single chemical compound like sugar or cellulose; we cannot write a chemical formula for protoplasm. Rather is it a mixture of many different compounds, including water, carbohydrates, fatty substances, proteins, and compounds of phosphorus and sulphur and of the metals calcium, potassium, magnesium, and iron. Usually 80 per cent, by weight, or more of protoplasm is water. Proteins rank second among the components of protoplasm. Familiar examples of proteins are gelatine and egg white. In addition to carbon, oxygen, and hydrogen, the proteins always contain nitrogen, generally sulphur, and sometimes phosphorus also.

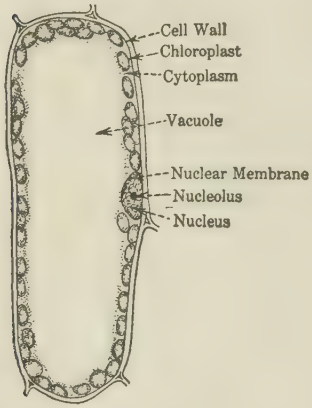


FIG. 13. A cell from the palisade parenchyma of a leaf.

The different parts of the protoplast and their relation to each other are shown in the following outline:

- The Protoplast
  - Cytoplasm
    - Cytoplasmic membranes
    - General cytoplasm including
      - Plastids
        - Leucoplasts
        - Chloroplasts
        - Chromoplasts
      - Chondriosomes
  - Nucleus
    - Nuclear membrane
    - Nuclear sap
    - Nucleoli
    - Nuclear net

The Cytoplasm.—Except in certain very simple plants such as bacteria there is in the protoplast of every typical cell a spherical

or oval structure called the **nucleus.** All the protoplasm outside of the nucleus is called the **cytoplasm.** Embedded in the cytoplasm are non-protoplasmic bodies of a number of different kinds. They are called **inclusions.** They may be drops of a watery solution of various substances, or crystals, or solid bodies of various non-crystalline forms, such as starch grains and protein granules. Where the cytoplasm is in contact with the cell wall there seems to be a thin layer having quite different properties from the rest of the cytoplasm. For this bounding membrane we shall use the term **cytoplasmic**

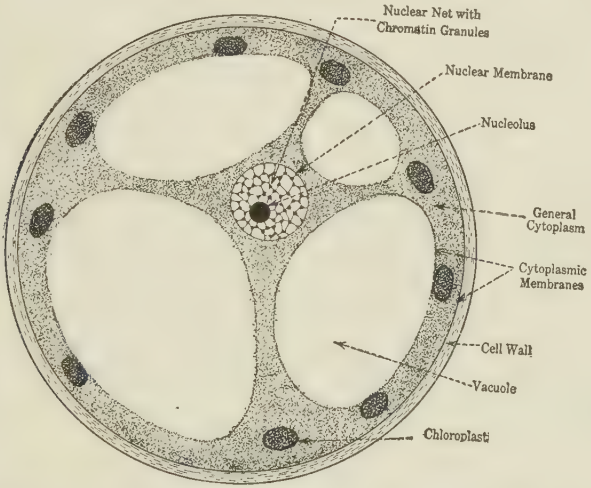


FIG. 14. Diagram of a single-celled (unicellular) green plant, showing the cell wall, the vacuoles, and the relation of the different parts of the protoplast.

membrane. Where the protoplasm is in contact with a vacuole there is a similar cytoplasmic membrane. These membranes are thought to be of great importance because they are believed to control the entrance and exit of substances into and from the cell. They are **semi-permeable membranes,** or, better, **differentially permeable membranes,** that is to say, membranes which permit the free passage through them of water and of certain substances in solution, but which prevent, or at least very greatly hinder, the passage of certain other substances in solution.

Plastids.—With the exception of certain reds and purples, the colors of flowers and fruits and leaves are due to pigments (colored compounds) which occur in specialized, living, cytoplasmic bodies

called **plastids.** These are generally spherical or ellipsoidal in form and may be considered merely as portions of the cytoplasm which are specially differentiated to perform particular functions in the cell. The plastids are of three kinds, which differ in color and in the nature of the work they perform: **chloroplasts,** green; **leucoplasts,** colorless; and **chromoplasts,** which are of various degrees or combinations of yellow, brown, or red.

Chloroplasts owe their characteristic color to the presence of a pigment called **chlorophyll** (Greek, *chloros*, green, + *phyllon*, leaf). This pigment is a mixture of two compounds, **chlorophyll *a*** ($C_{55}H_{72}O_5N_4Mg$), and **chlorophyll *b*** ($C_{55}H_{70}O_6N_4Mg$). Associated with them in the chloroplast are two yellow pigments, **carotene** ($C_{40}H_{56}$), and **xanthophyll** ($C_{40}H_{56}O_2$). Though not a component of chlorophyll, the element iron must be present in the plant for the formation of chlorophyll. The quantity and intensity of the green pigments largely mask the yellow pigments, although these do alter the color of the chloroplasts. It is the chloroplasts which give the color to the green cells of leaves and of the young parts of many stems. Organs which do not normally possess chloroplasts, such as the tubers of the potato, may develop green plastids when exposed to the light. In such cases, leucoplasts which were present in the cells before exposure to light are stimulated to produce pigments and are thus transformed into chloroplasts.

The green plastids are the centers of the process of photosynthesis, by which the simple compounds carbon dioxide and water, secured from the air and from the soil, are built up into sugar and starch. Leucoplasts are always present in cells in which starch is stored, such as those of starchy seeds, of the potato tuber, and of starch-storing roots like the sweet potato. They are able to change certain sugars (soluble carbohydrates) into starch. The starch is built up inside the leucoplasts into starch grains. As these grains increase in size the leucoplasts stretch to many times their original dimensions.

Chromoplasts are responsible for the red, yellow, orange color of many flowers and fruits. The petals of such flowers as mustard, gaillardia, dandelion, sunflower, etc., the skin of the orange, the flesh of tomato, the outer coats of yellow corn grains—all owe their color to chromoplast pigments, chiefly carotene and xanthophyll.

Carotene was so named because of its abundance in carrots and the fact that the characteristic color of ordinary carrots is due to this compound. It is of interest that vitamin A seems to be associated with carotene and xanthophyll in leaves which are rich in chlorophyll; it is also abundant in carrot roots and in yellow corn. It is likewise of interest to know that carotene and xanthophyll, unlike chlorophyll, are not changed in the digestive tract of animals. The yellow color of the yolk of eggs is due to these pigments; and, if hens are fed white corn, instead of yellow, and are prevented from getting green foods, in which a considerable quantity of carotene and xanthophyll occur along with the chlorophyll, the yolks of the eggs which they lay will be pale in color.

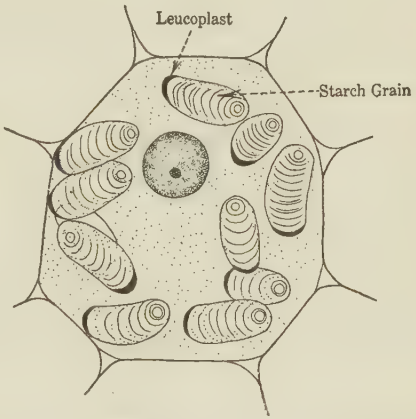


FIG. 15. Starch-storing cell of *Pellionia* showing leucoplasts and starch grains. Note that starch grains are formed within the plastids. (Redrawn from Gager.)

A single plastid may be in turn a leucoplast, a chloroplast, and a chromoplast. This is the case in the cells of many fruits, such as the red pepper or tomato. In the young flower of these plants, the ovary, that part of the flower which develops later into the fruit, is almost colorless and the cells near the surface contain numerous leucoplasts. Later, the ovary, as well as the young fruit which develops from it, will become green; chloroplasts will be found to have developed from the leucoplasts. As the fruit ripens, the chloroplasts are transformed to chromoplasts and the color of the fruit changes from green to red.

In many cases the color of flowers and fruits is due, not to pigments contained in plastids, but to colored substances dissolved in the solution (cell sap) contained in the vacuoles of the cells. The two methods of coloration, by chromoplasts and by dissolved pigment, are sometimes combined even in a single cell.

Small rod-shaped bodies, granules, or filaments are found in the cytoplasm of the cells (particularly young cells) of both plants and animals. They are called **chondriosomes** or **mitochondria**. Special

staining methods are necessary to make them visible. Though of almost universal occurrence, there is no general agreement among cytologists as to their nature and function.

The Nucleus.—The nucleus is believed to control all the activities which go on in the living cell. There is abundant evidence that it is material within the nucleus which is principally responsible for the fact that organisms inherit the characteristics of their ancestors. Typically the nucleus is a spherical structure, although ellipsoidal, disk-shaped, or considerably elongated nuclei occur. It appears to be surrounded by a definite **nuclear membrane** and contains a highly transparent material called the **nuclear sap.**

Within the nucleus are the **nucleolus** (plural, **nucleoli**) and the **nuclear net.** The nucleolus is another cell structure concerning the function of which opinions differ. Usually the nucleus contains one nucleolus, but two or more may occur in a single nucleus, and in some nuclei they are lacking altogether. Nucleoli are generally spherical in form. At an early stage in the division of the nucleus at the time of cell division, the nucleoli disappear entirely, but they are formed again in the two new nuclei.

The so-called **nuclear net** appears to consist of granules scattered here and there along threads which form a network. The material of these granules is called **chromatin,** and to the material of the network the name linin is often applied. Chromatin is without question a substance of very great importance. There is conclusive evidence that it is this substance which bears the characteristics which the plant is able to pass on to successive generations. There can be no doubt that the resemblance of a plant to its parents is largely due to the fact that in the process of reproduction some of the chromatin of each parent plant is contributed to the new individual.

It should be borne in mind that the general term living substance, or protoplasm, comprises all the material of the cell except such dead inclusions as vacuoles, starch grains, and crystals.

Vacuoles.—The vacuoles are drops of liquid found in all but the very youngest cells. The name **cell sap** is applied to the contents of the vacuole. As the cell grows, the vacuoles increase in size and some of them come into contact with each other and fuse. Thus they

become fewer in number but larger in size in the older cells than in the younger ones. By the time the cell has reached its greatest size there is generally only a single large vacuole. Since this is commonly larger in volume than the protoplasm and occupies the center of the cell, the protoplast in old cells has the form of a closed sac. In such cells the nucleus lies near the cell wall, embedded in the cytoplasm, or is suspended in the large central vacuole by fine threads of cytoplasm which are connected with the cytoplasm lining the cell wall. In the latter case also the nucleus is surrounded by a layer of cytoplasm. It is never in direct contact with the vacuole or the cell wall.

The liquid within the vacuole is not pure water, but a solution of many substances dissolved in water. Among these substances are the gases of the atmosphere, including nitrogen, oxygen, and carbon dioxide; inorganic salts (such as nitrates, chlorides, sulphates, or phosphates of the metals potassium, sodium, calcium, or magnesium); organic acids (such as malic, tartaric, citric, formic, acetic, and oxalic); compounds of some of these acids with the metals named above; sugars (such as cane sugar and grape sugar); and other substances. In many plants the cell sap of certain cells contains dissolved anthocyanin pigments which give a red, purple, or blue color to the organs or tissues in which it occurs. The common red beet owes its colors to such pigments dissolved in the cell sap.

In addition to vacuoles containing a watery cell sap, there occur in certain cells oil drops of considerable size which are sometimes spoken of as oil vacuoles. The oil reserve in the seeds of castor bean, peach, juniper, and many other plants may be seen in the form of large drops in sections of such seeds examined under the microscope. However, not all fatty substances in plants occur as drops. Fats sometimes are found in the cell walls, or are so homogeneously mixed with the protoplasm that oil vacuoles cannot be demonstrated.

Crystals.—Crystals of calcium oxalate, calcium carbonate, and, less frequently of other substances, can be found in almost all plants. They occur in the vacuoles of mature cells. The crystals may be large ones occurring singly, numerous very fine ones scattered through the cytoplasm, bundles of fine sharp needles, or spherical groups of radiating crystals.

Starch Grains.—Next to cellulose, starch is the most abundant carbohydrate in the plant kingdom. It is the principal form of carbohydrate stored in plants. It occurs in the greatest amounts in seeds (e.g., wheat, oats, barley, corn, rice), tubers (potato), and roots (sweet potato, parsnip, etc.), and is found in the green cells of most plants after a period of active food manufacture. The stored starch of plants is one of the most important substances used as food by the higher animal.

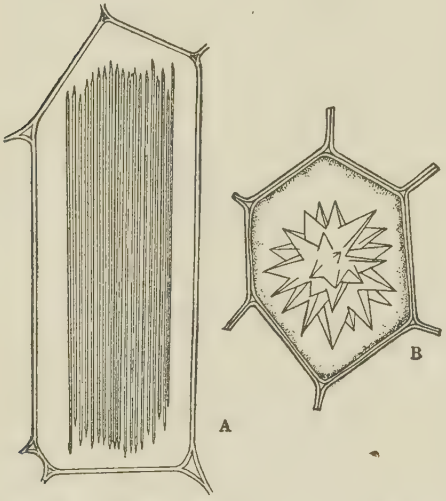


FIG. 16. Crystal inclusions. *A*, a cell from the stem of spiderwort (*Tradescantia*) showing a group of raphides. *B*, a cell from the leaf-stalk of dock (*Rumex*) showing a crystal cluster. In *A* the cytoplasm has been omitted.

Starch occurs in the plant in the form of grains. In the leaves these grains are formed within the chloroplasts. The grains of reserve (stored) starch consist of successive layers which are often thicker on one side of the grain than on the other. This is conspicuously the case in the starch grains of potato. The starch molecule consists of carbon, hydrogen, and oxygen atoms united in the proportions of six of carbon to ten of hydrogen and five of oxygen, but the molecule contains a very large number of atoms. Starch grains are themselves insoluble in water, but are capable of conversion into certain sugars which are soluble. This conversion of starch to sugar (digestion of starch) is aided by an enzyme called amylase (or diastase) produced by the plant itself.

When a green leaf cell containing starch discontinues food manufacture, as it does when night comes on, the starch is changed into sugar (digested) and passes to parts of the plant where it will be used or stored. The sugar which reaches the storage organs may be stored in the cells in the form of sugar, as in the sugar beet, or may be converted again by leucoplasts into starch and remain in this form until it is needed by the plant. It is then changed back into

sugar and passes to the parts of the plant where it is to be used as food. Thus, when a potato tuber sprouts, its stored starch is largely changed to sugar which is used in the growth of the sprouts.

When starch grains are treated with a solution of iodine they become blue in color. The form of the grains of reserve starch is different in different plants, a fact which often makes it possible to determine, by microscopic examination of a sample of starch, from what kind of plant it was secured.

The two greatest sources of commercial starch are the potato tuber and the corn kernel. Starch can be converted into a variety of products for industrial and dietary uses. Corn starch is the basis of commercial glucose or corn syrup, which is a mixture of three starch derivatives, namely, maltose, dextrose, and dextrin. Dextrin is used for the mucilage on envelopes and postage stamps. Dextrose can be converted by fermentation into alcohol.

FUNCTIONS OF THE CELL

It is to be borne in mind that every function which the plant performs is but the expression of the activities of individual cells. In one-celled plants all the essential life processes may be carried on within a single protoplast. The principal processes which may go on in the cell are **absorption, synthesis of foods, digestion, assimilation, respiration, growth,** and **reproduction.** Let us consider a one-celled green plant freely floating in water. It **absorbs** water containing in solution various salts and gases; it **builds up** or **synthesizes** from the absorbed materials different foods, such as sugars, starch, fats, and proteins; and, if certain of the stored foods are in an insoluble form, starch for example, the cell must **digest** these foods before they can be utilized, that is, change them into soluble substances. The cell also **assimilates** food—converts it into living material (protoplasm); it **respires,** or breaks down food (sugars, chiefly) into simpler chemical forms, thereby liberating the energy stored in such foods, which energy is then available to do the work of the cell; it **grows,** by adding to its protoplasm and to the thickness of its wall; and finally it **reproduces,** that is, divides into two cells which separate to form two unicellular plants.

Absorption.—*Solution.*—It is impossible for substances to enter the plant cell unless they are in solution in water. Except where

otherwise stated, the term solution, when used in this book, is to be understood as designating a true solution. A true solution is a mixture in which none of the component particles are larger than molecules. For example, if a small quantity of pure sodium chloride (table salt) is added to pure water, it forms a true solution, that is, the molecules of salt become separated from one another and uniformly distributed through the water. In this example sodium chloride is the **solute**, water the **solvent**, and the **solution** is the system in which the solute is distributed throughout the solvent in the form of molecules or molecules and ions. The gases of the atmosphere, including oxygen and carbon dioxide, are absorbed by plants, but they must also first go into solution in water before actually entering the cells. All other substances are absorbed from the water solution in the soil. In many unicellular aquatic green plants, such as certain algae, all materials, including oxygen and carbon dioxide, are absorbed from the water (sea, stream, lake, pond) in which they are submerged. Soil water, sea water, and waters of rivers, lakes, and ponds are generally very dilute solutions.

FIG. 17. Diagrammatic representation of the diffusion of dissolved particles from a crystal undergoing solution in water.

Diffusion.—This is a process which plays a very important part in the physiology of plants and animals. If a piece of some deeply colored soluble substance such as blue vitriol (copper sulphate) is dropped into a glass of water, it will gradually go into solution. For some time, however, the solution will be more deeply colored in the vicinity of the solid fragment, indicating that the colored component of the solution is more concentrated (that is, the dissolved particles of the solute or dissolved substance are more crowded or nearer together) there than in more distant parts of the solution. In time the whole solution will become uniform in color, indicating that the dissolved particles of the solute have become uniformly distributed among the water particles.

Such scattering of the particles of one component of a solution among those of the other components, resulting in a uniform distri-

bution of the particles of all components throughout the solution, is called **diffusion.**

Diffusion of solutes in liquids is not a rapid process, and when we make a solution we do not ordinarily wait for diffusion to become complete, but hasten it by shaking or stirring.

Passage of Solvents through Membranes.—If water is carefully poured upon a quantity of sugar syrup (a concentrated solution of cane sugar and water) the two fluids will at first form two distinct layers. Soon, however, the molecules of water will diffuse into the concentrated sugar solution and those of the sugar will diffuse into the water, so that finally a uniform solution results. If the syrup and water are separated by a membrane like an ordinary cell wall through which water and the dissolved particles of sugar can pass freely, water will diffuse into the syrup and sugar into the water so that the solutions on the two sides of the membrane will become equal in concentration. Such a membrane which permits water and all solutes to pass freely through it is called a **permeable membrane.**

It is possible to prepare membranes which permit water to pass freely, but restrict or prevent the passage of some or all solutes. Such a membrane is generally called a **semi-permeable membrane,** although a better term would be **differentially permeable membrane.** Reference has already been made to the natural occurrence of such membranes in living cells.

When pure water or a dilute solution is separated from a concentrated solution by a semi-permeable membrane through which the solute cannot pass, an interesting situation results. This will be easier to understand if we think of the membrane as stretched across the U-shaped tube shown in Fig. 18.

The left-hand arm of the tube in *A* is partly filled with a solution of 5 grams of cane sugar in 100 cubic centimeters of water. The right-hand arm contains a dilute solution, let us say of 1 gram in 100 cubic centimeters of water. The level of the liquids in the two arms of the tube is the same, and the semi-permeable membrane, through which sugar cannot pass, separates the two solutions.

Now water diffuses from the more dilute solution on the right through the membrane to the more concentrated solution on the left.

The solute, cane sugar, *tends* on the other hand to diffuse from the more concentrated solution on the left of the membrane to the

more dilute solution on the right. **The cane sugar will not pass, however, because the membrane is not permeable to it.** As a consequence of water passing through the membrane from right to left the following changes occur:

1. The volume of the solution in the right arm becomes less as the result of the loss of water. The concentration of the solution in the right arm becomes greater for the same reason.

2. The solution in the left arm becomes more dilute as the result

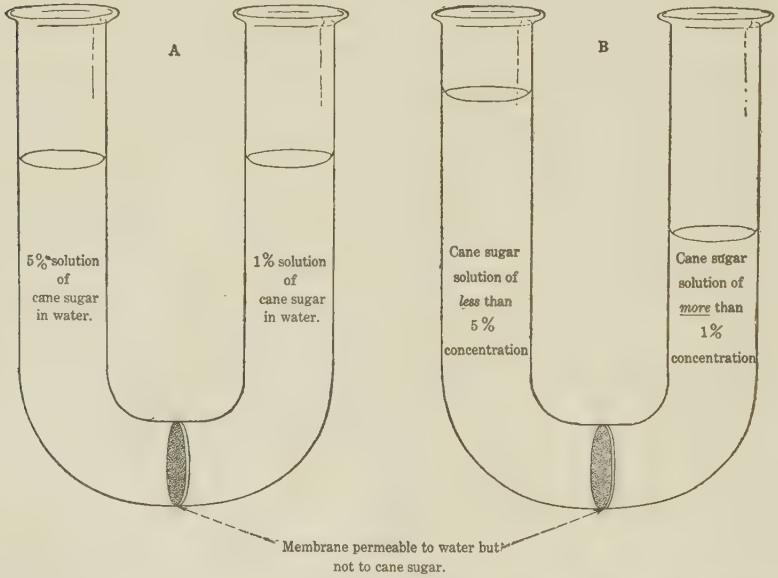

A
B
5% solution of cane sugar in water.
1% solution of cane sugar in water.
Cane sugar solution of less than 5% concentration
Cane sugar solution of more than 1% concentration
Membrane permeable to water but not to cane sugar.

FIG. 18. Diagram illustrating diffusion through a semi-permeable membrane. For explanation see text.

of the addition of water from the other arm. Its volume becomes greater for the same reason.

3. The level of the solutions becomes different, as shown in *B*, the level rising in what was originally the more concentrated solution and falling in what was originally the more dilute.

The difference in level of the solutions in the two arms of the U-tube forces us to the conclusion that there is a pressure supporting the column which stands at the higher level. This pressure is called **osmotic pressure.**

It should be borne in mind that, when two solutions are separated

by a membrane, water will pass from one of the solutions to the other and give rise to osmotic pressure only if:

1. The membrane is permeable to water.
2. A solute or solutes are present which cannot pass freely through the membrane.
3. The total number of dissolved particles of the solute in a given volume of the solution is greater on one side of the membrane than on the other.

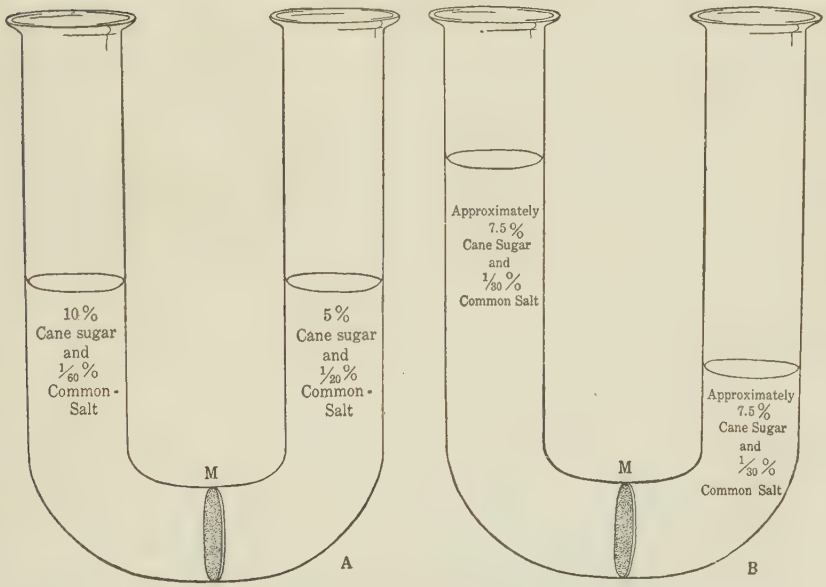

10% Cane sugar and 1/60% Common Salt
5% Cane sugar and 1/20% Common Salt
M
A
Approximately 7.5% Cane Sugar and 1/30% Common Salt
Approximately 7.5% Cane Sugar and 1/30% Common Salt
M
B

FIG. 19. Diagram illustrating diffusion through a semi-permeable membrane. For explanation see text.

Diffusion of Solutes.—Figures 18 and 19 illustrate the passage of the solvent through a semi-permeable membrane. Figure 19 shows, in addition, the diffusion of one of the solutes. Most semi-permeable membranes permit the dissolved particles of some dissolved substances (solutes) to pass freely but are relatively impermeable to those of other substances. The membrane separating the two solutions in Fig. 19 is such a **selective** membrane; it is permeable to water and to common salt, but not to cane sugar. As in the former example, the result of diffusion was the establishment

of relative uniformity of concentration in both arms of the U-tube. But whereas the salt content was equalized by the passage of salt particles from the arm where the salt was more concentrated to the arm where the salt concentration was less, equal distribution of the sugar was brought about by the passage of water from the arm where the concentration of sugar was less to the arm where the concentration of sugar was greater, thus raising the level of what was originally the more concentrated solution.

Diffusion in Relation to Absorption by the Plant Cell.—Nothing can pass through the cell wall or enter the cytoplasm unless it is in true solution in water. The cellulose wall surrounding the protoplast is a permeable membrane and in general cannot impede the passage, inward or outward, of any of the substances dissolved in the cell sap or in the water surrounding the cell. The cytoplasmic membrane, on the other hand, is semi-permeable. It freely admits, from outside the cell, water and many of the substances dissolved in it, but restricts the outward passage of most of the solutes in the cell sap. There are many factors, such as temperature, light, and various electrolytes and non-electrolytes, which affect the permeability of cytoplasmic membranes, so that substances admitted at one time may be excluded at another.

The total concentration of dissolved substances is normally much greater in the cell sap than in the solution outside the cell. In the latter, however, certain solutes (considered by themselves) will be present (dissolved) in greater concentration than in the cell sap. In the light of the foregoing explanations, it will be understood that the cell will tend to absorb from without: (*a*) water; and (since the diffusion of a solute inward may be independent of other solutes present) (*b*) some of the solutes in the solution outside the cell.[1]

[1] In general, water or any of the solutes present outside the cell will tend to pass into the cell if the cytoplasmic membrane is permeable to it and if it, considered by itself, is more concentrated in the solution outside the cell than in the sap. Thus there would tend to be a uniform distribution, inside and out, of every substance (water and each solute) to which the cytoplasmic membrane is permeable.

It has been shown that not only simple, single-celled organisms immersed in a solution, but also the root cells of higher plants, absorb nutrients actively and build up within their vacuoles concentrations many times that of the external solution. This cannot be explained by the simple diffusion theory, and most botanists now accept the **theory of active solute absorption.** This theory asserts that living cells absorb and accumulate certain solutes by forcing the dissolved particles to move from a

The water taken in by the cell (*a*) tends to enlarge the vacuole by increasing the volume of the cell sap, and (*b*) also permeates the protoplasm (perhaps somewhat as gelatine or glue absorbs water and swells), causing it to swell. Largely owing to the former, the cell is distended, the cytoplasm being pressed outward against the cell wall, and the cell becomes rigid, somewhat as an inflated football. So great is this pressure (reaching 20 kilograms per square centimeter in the cells of the sugar beet with their highly concentrated cell sap) that it would burst the protoplast were it not for the mechanical strength of the cell wall and the pressure of surrounding cells, if such are present.

Every living plant cell, whether surrounded by other cells in a multicellular plant body or existing as an individual unicellular plant immersed in the water of a pond, is normally in such a state of inflation that it will lose some of the distending force (called turgor) when placed in a solution more concentrated (containing more dissolved particles of all solutes in a given volume) than its own cell sap. Some of the water will then pass outward through the cytoplasmic membrane, the vacuole will shrink, the cell will no longer be plump and distended, and the tissue will lose its rigidity. If loss of water continues until the protoplast pulls away from the wall, the condition is called **plasmolysis** (Fig. 20). When a lettuce leaf, crisp because of the high turgor pressure in its cells, is placed in a solution more concentrated than the cell sap, it wilts as the result of the reduction or complete loss of turgor pressure in its cells. The cell's power to grow in size is largely dependent upon the maintenance of considerable turgor in the cell.

In mastering these processes of absorption (and all other functions) of the cell, the student should guard against an error which often results from the necessity of describing and explaining each part of the process, or each process, singly and separately. This error is failure to realize that in the living plant, even in each living cell, many processes are going on simultaneously. Thus an absorbing

solution where they are less abundant, across the protoplasmic layer into the cell sap, where they reach relatively high concentrations. This is accomplished by an expenditure of energy and constitutes a considerable portion of the labor which plant cells are required to perform. Experiments have shown that high absorption rates are usually attended by high respiration rates, and it seems logical to assume that this respiration provides the energy required for absorption and accumulation.

cell, for example one of those on the surface of a root (elongated into a root hair), may at one and the same time be admitting water, taking in several different solutes at different rates, and also giving out carbon dioxide, one of the few solutes which can be given off by living plants.

Photosynthesis and Respiration.—The protoplast absorbs substances from outside of itself and makes these substances into the material of its own body. From the substances absorbed, it first builds or synthesizes foods, and then changes these foods into

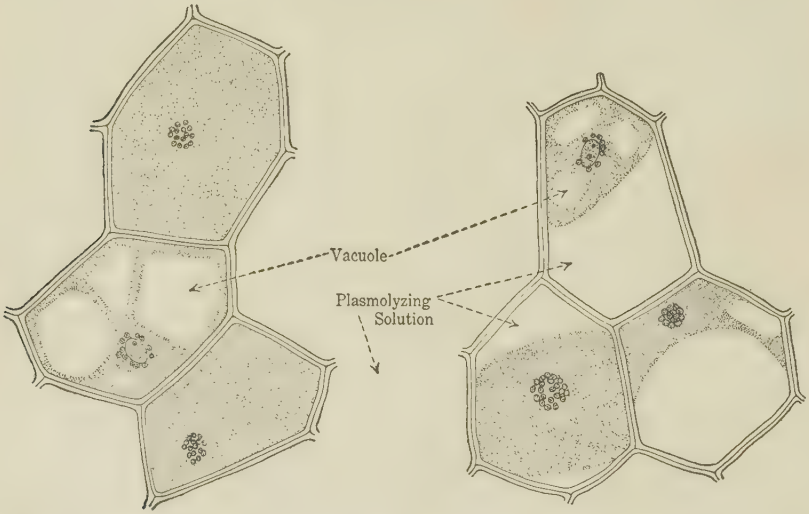


FIG. 20. Plasmolysis of epidermal cells of wandering Jew (*Zebrina pendula*). *A*, cells in water. *B*, cells after brief immersion in 20 per cent solution of cane sugar. Note that the spaces between the cytoplasm and the cell wall in the plasmolyzed cells are filled with the solution in which the cells are immersed. In each drawing two cells are shown as seen in surface view and one in section.

protoplasm, cellulose, and other plant materials. We shall use the term food only for those materials which are capable of yielding energy when respired (oxidized within the plant) and which may be utilized, without any considerable change, as building material for the protoplasm. The principal classes of food are carbohydrates, fats, and proteins. For substances like water, carbon dioxide, and inorganic salts which the plant can utilize for the manufacture of foods but which cannot be respired, we shall use the expression **raw materials for food manufacture.**

The energy needed by the cell for the performance of its functions—which means doing work—is derived from the sun. When

illuminated, under natural conditions, by sunlight, all cells containing chlorophyll have the power of uniting water and carbon dioxide to form glucose, which is a soluble carbohydrate or sugar. This is the process of **photosynthesis.** It will be treated more fully in connection with the physiology of the leaf. The plant is able to make fats from the sugar produced in photosynthesis and proteins from sugar and certain solutes absorbed from the soil.

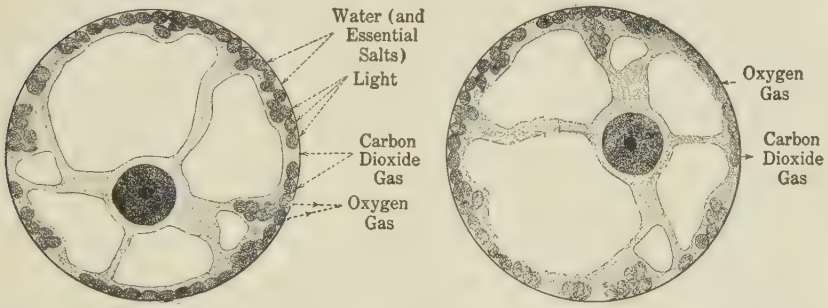


FIG. 21. Left, diagram of a unicellular, aquatic plant showing the absorption of materials and energy essential to photosynthesis, and the liberation of oxygen which takes place during the process. No attempt has been made to represent the carbohydrate (starch or sugar produced within the cell by photosynthesis). Right, diagram of a unicellular, aquatic plant showing the gas interchange during respiration. In addition to carbon dioxide gas, water is also a product of respiration.

The **solar energy** absorbed in photosynthesis is stored in the glucose as **chemical energy.** Thus solar energy is transformed into chemical energy. Part of this is liberated again when, in the process of **respiration,** the glucose, or related substances produced from it, is broken down again into water and carbon dioxide. The energy thus liberated is used in various processes in the plant. As respiration requires no supply of energy from without, it can, and in fact does, go on continuously in all living cells.

Digestion.—Some of the foods produced by the plant are stored temporarily in certain cells in insoluble form. Fat globules, grains of starch (an insoluble carbohydrate), and certain proteins are examples of such insoluble foods. Since only substances which are in solution in water can move from one cell to another, it is necessary to convert these insoluble substances into soluble substances when they are to be used. This change of insoluble foods into soluble foods is called **digestion** and is an important process in plants as well as animals.

Assimilation.—The conversion of carbohydrates, fats, proteins, and simpler nitrogenous foods into the living material (protoplasm) of the cell is called assimilation. Assimilation is a synthetic process, the chemical reactions involved being chiefly condensations of simple foods to complex cell constituents. It is a process about which we can know very little until we understand much better than at present the nature of the protoplasm itself.

Growth.—Growth of the cell results in part from the increase in the quantity of protoplasm (by assimilation), and in part from absorption of water into the cell and a stretching of the cell wall due to the resulting turgor. During growth, sugar is converted into cellulose by the protoplasm lining the cell wall. Thus the thickness of the cell wall may be increased. The growth of a multicellular plant differs from that of a unicellular one in that it involves not only increase in the size of cells, in the quantity of protoplasm, and in the thickness of cell walls, but also increase in the number of cells.

Growth Hormones.—Substances called **growth substances, growth hormones,** or **phyto-hormones** are known to occur in a great variety of plants. They often influence organs of the plant other than those in which they are produced, and peculiarly only extremely minute quantities are required to produce an effect. The best-known plant hormones are the **auxins.** Interesting experiments have been carried on using the leaf-sheath (coleoptile) of oat seedlings. The growth of this organ is at the base; but the hormone necessary for the growth of the basal region originates in the cells at the tip of the sheath, and moves from tip cells to basal cells, upon which it exerts an influence resulting in their growth. Chemically pure crystalline substances with the properties of auxins have been isolated. Chief of these are auxin *a*, prepared from human urine, malt, and various vegetable oils; auxin *b*, isolated from malt and certain vegetable oils; and hetero-auxin (indole-acetic acid), isolated from urine, certain yeasts, and molds. The latter is also prepared synthetically and sold on the market as a growth-promoting substance.

Auxins are apparently necessary to stimulate cell elongation in roots, as well as in other organs of the plant. Thus, root elongation is favored by very low concentrations of auxins. Moreover, the initiation of roots on cuttings is favored by the presence of auxins;

such auxins are produced in the young leaves and buds of the cuttings and moved to the basal part. In practice the basal ends of cuttings are immersed in an aqueous solution of the auxin for approximately 24 hours, with the result that root formation is speeded up, and also a larger number of roots are produced.

Factors Influencing Growth.—The growth of a cell, or of an organ, or plant as a whole, is influenced by a number of factors. First of all are the hereditary factors; we recognize that it is the nature of some plant species to grow slowly, of others to grow rapidly, under the same environmental conditions. Since growth is in part the resultant of all activities of the plant, the factors affecting these various activities exert a more or less direct influence on growth. We may mention among such factors: temperature of the soil and air, light, atmospheric humidity, water in the soil, air in the soil, concentration of mineral salts and gases of the soil, gravity, and atmospheric pressure. These factors are discussed briefly in subsequent chapters.

Multiplication of Cells.—After attaining a certain size the unicellular plant divides into two cells, which then separate, and each after a period of growth repeats the process. In multicellular plants this power of repeated division is restricted to certain cells.

Cell division is a process in which there is a definite sequence of complex changes. First a division of the nucleus into two daughter nuclei takes place. Immediately thereafter the cytoplasm is divided by a membrane formed between the two daughter nuclei. This is the middle lamella, and upon it the two new protoplasts deposit the cellulose which soon makes up the greater part of the dividing wall. This procsss of cell division is of such great importance that a more detailed description is necessary.

A resting nucleus, that is, one not in a state of division, has already been described. In such a resting nucleus there appears to be a network of threads to which material the name linin is sometimes given. Along the strands of the net there occur here and there chromatin granules. At the beginning of nuclear division the chromatin granules come together and take on the form of a thickened thread which is irregularly coiled. This is called the **spireme.** Then the thread splits lengthwise into two strands which, however, remain very close together. After this, the double thread

shortens and breaks up transversely into segments or rod-shaped pieces, each still consisting of two strands. These segments are called **chromosomes**. In all cells of the individuals of a given species, except certain reproductive cells, the number of chromosomes which appear at the time of nuclear division is the same; in these reproductive cells the number is one-half that in the nuclei of the ordinary cells.

While these changes have been going on in the nucleus there arise in the cytoplasm immediately surrounding the nucleus two groups of delicate fibers, which radiate toward the nucleus from two centers, situated on opposite sides of the nucleus. The nucleoli and the nuclear membrane now disappear, and the fibers extend to the middle of the nucleus, where some of them become attached to the double chromosomes, and others connect with fibers radiating from the opposite pole, so that there are some unbroken fibers extending from pole to pole. The two cones of fibers meeting near the middle (equator) of the nucleus form the **spindle**.

Now, the double chromosomes become arranged in a plane at the equator of the cell halfway between the two extremities (poles) of the spindle. The halves of the longitudinally split chromosomes attached to spindle fibers separate and move towards opposite poles. Thus there are formed two groups of daughter chromosomes, one at each pole, with equal numbers of daughter chromosomes in each group. Soon, the chromosomes of each group begin to spin out into the form of a nuclear net, nucleoli appear in both nuclei, and thus two new daughter nuclei are formed, similar to the parent nucleus.

During this reorganization of the two daughter nuclei, the spindle fibers which extend from pole to pole begin to thicken at the equator; then they spread out and come into contact with the lateral walls of the mother cell. On the thickened fibers at the equator, swellings now appear, which increase in size and finally fuse, thus forming a continuous plate (the **cell plate**), which extends across the equator of mother cell and divides it into two daughter cells. The fibers then disappear altogether.

It should be added at this point that, after the origin of the cell plate, this structure splits and forms the cytoplasmic membranes of the two daughter cells. Between these two membranes is secreted the material which makes up the middle lamella.

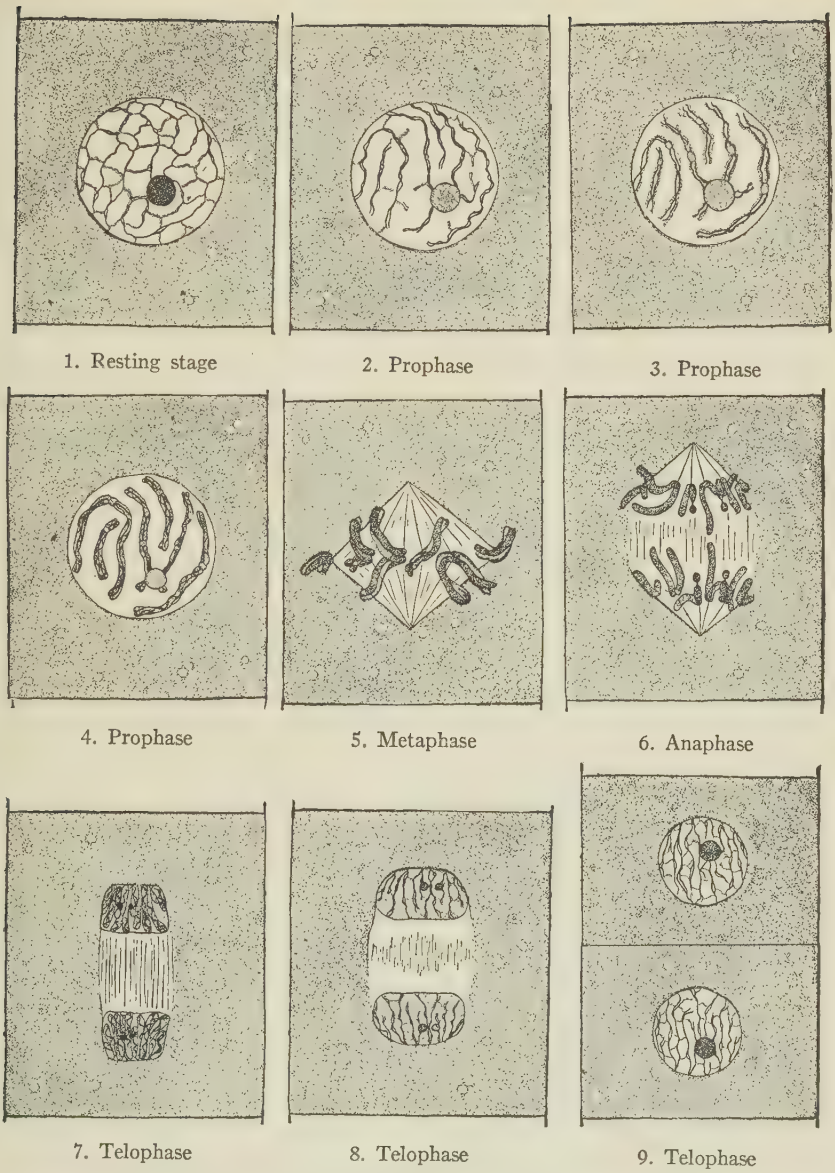


FIG. 22. Semi-diagrammatic representation of cell division in meristematic cells of a plant, showing nuclear division by mitosis. 1, Cell before division begins, with the nucleus in the resting condition. The chromatin threads form a network. 2, 3, 4, Prophase of nuclear division. In 2 and 3 the double nature of the chromatin threads is apparent. In 4 the chromosomes are distinct and their doubleness still apparent. 5, Metaphase of nuclear division; nucleolus and nuclear membrane have disappeared, the spindle has been formed, the chromosomes lie in or near the equator of the spindle, and some of the fibers are attached to the chromosomes. 6, Anaphase. Movement of daughter chromosomes away from the equator of spindle. 7, 8, 9, Telophase. In 7, daughter chromosomes form two compact masses. 8, Reorganization of resting nuclei begun, the double nuclear threads become apparent, nuclear membrane and nucleolus appear. In 9 the nuclear net is forming and the new cell wall separates the two new cells. (The nuclei redrawn from a figure in Sharp's *Introduction to Cytology*, 3rd Edition, McGraw-Hill Book Co.)

CHAPTER IV

THE STEM

Most land plants—the common trees, shrubs, and herbs—bear their leaves and flowers on stems which raise these organs well above the surface of the soil. Consequently, it is necessary that such stems have sufficient strength to maintain an erect position and bear their burden of leaves, flowers, and fruit, and, moreover, that they possess tissues which are capable of conducting water and certain raw materials for food manufacture to the leaves, and food from the leaves to other parts of the plant. It is clear that the chief functions of stems are support and conduction. A study of their structure will show how they are adapted to carry on these functions.

THE DICOTYLEDON TYPE OF STEM

Many structural features are common to both herbaceous and woody stems. In order to understand the structure of the stem, it will be necessary to examine and study with the microscope both cross and longitudinal (lengthwise) sections. Moreover, these sections must be taken at various distances from the stem tip in order to show the stages in development. It should be constantly borne in mind that the greater distance any portion of the stem is from the growing point in the terminal bud, the older it is. A section of the terminal bud, made lengthwise through the center, shows us many important features of stem structure. At the very tip is the growing point, a cone-shaped mass of meristematic tissue, a type of tissue which is generally compact and without any intercellular spaces between the cells. The cells are thin-walled and seldom much longer than wide. The nucleus makes up a large part of the volume of the protoplast, and the vacuoles are either absent or very small. Meristematic cells are essentially all alike. Their most important characteristic is the capacity for repeated division. In fact, the growth in length of the stem would not be possible without the

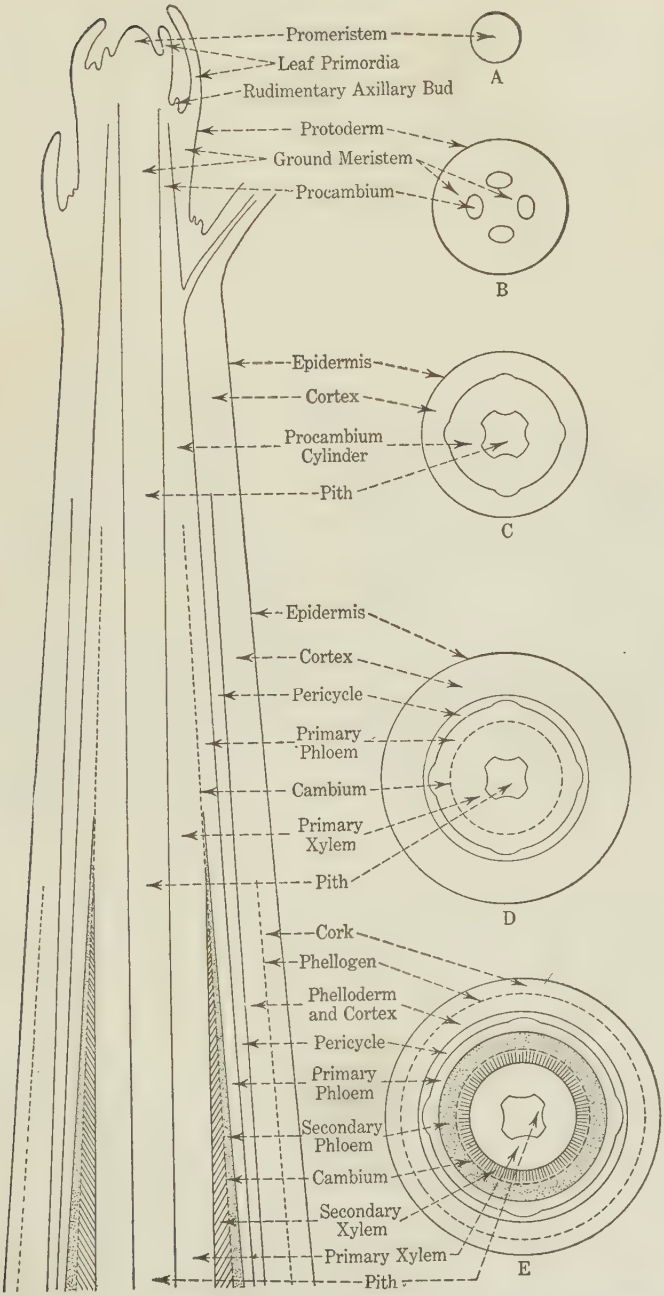
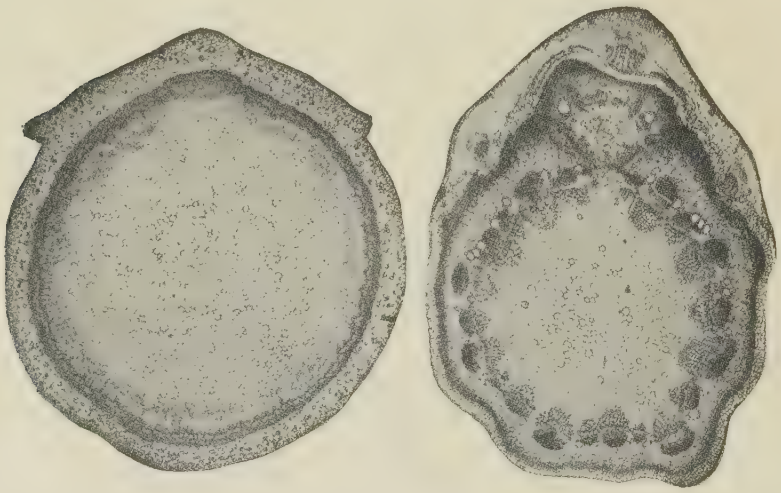


FIG. 23. Diagram of longitudinal and cross sections of a woody dicotyledonous stem, showing primary and secondary growth.

addition of new cells by the meristematic tissue of the growing point. These meristematic cells of the growing point constitute a tissue known as the promeristem or primordial meristem.

Passing downward from the very tip of the stem, four growth regions or zones may be recognized: (1) a region of meristematic activity with slight growth in length, which includes the promeristem, (2) a region of active elongation, (3) a region of differentiation of tissues in which there is little elongation, and (4) a mature region, making up the rest of the stem, in which there is no elongation



A *B*

FIG. 24. Types of dicotyledonous stems (continued). Herbaceous stems. *A*, with continuous vascular cylinder, *Digitalis*, and *B*, with distinct vascular bundles, *Artemisia*. (After Sinnott and Bailey, from Eames and MacDaniels, *Introduction to Plant Anatomy*, McGraw-Hill Book Co.)

whatever. The first region makes up most of that part of the stem which is within the bud and generally includes several young nodes and internodes. The region of active elongation extends from the base of the bud downward through several more nodes and internodes. The rapid growth in length in this region is due to the fact that the relatively short cells of the first region, which have no vacuoles or very small vacuoles developing, take up large quantities of water so that the cells stretch lengthwise as a result of high turgor. Growth in length of the stem is due principally to such stretching

of the cells of successive internodes rather than to elongation of the nodes.

Growth in length of stems may be very rapid. The stem of bamboo probably holds the record, the total increase in stem length being as much as 2 feet in 24 hours. Squash stems are known to grow 6 inches during a 24-hour period.

Just back of the growing point, the cells produced by the promeristem have differentiated somewhat in size and shape to form three **primary meristems**, which can best be seen in a cross section of the stem. These are the **protoderm**, the **ground meristem**, and the **procambium strands**. The cells of the primary meristems continue for a time to divide, though less actively than those of the promeristem. By gradual loss of power to divide and by differentiation in form, thickness of wall, development of intercellular spaces, etc., they are converted into the so-called **primary permanent tissues**, which are tissues no longer capable of active cell division but fitted to carry on the various activities of the stem.

The protoderm is the outermost layer of primary meristem cells. It develops into the **epidermis**, a primary permanent tissue.

The ground meristem makes up the greater part of the tissue within the protoderm. It consists of relatively large, thin-walled isodiametric (having about the same diameter in all directions) cells, among which the intercellular spaces soon appear. It differentiates into the following primary permanent tissue groups: the **cortex**, the **pericycle**, the **pith rays** (if these are present), and the **pith**, which makes up the center of the stem.

When the procambium cells first become distinguishable from the promeristem they are often in strands, therefore appearing in a transverse section as isolated groups of cells. These strands are arranged in a circle. A little later more procambium cells may be formed between these strands until in many stems there is produced a continuous hollow cylinder (a ring in cross section) of procambium. In some stems the strands never join to form a hollow cylinder. From the procambium three tissue groups or regions are derived as differentiation goes on. These are the **phloem**, the **cambium**, and the **xylem**. Where the procambium strands do not join to form a **procambium cylinder**, the phloem, xylem, and cambium are

united in several separate strands which are called **vascular bundles** (see Figs. 24B and 25), and the cambium is spoken of as **fascicular cambium** (cambium belonging to a bundle). Where there is a procambium cylinder, the cambium forms a continuous ring with xylem on the inside of it and phloem on the outside. The cambium,

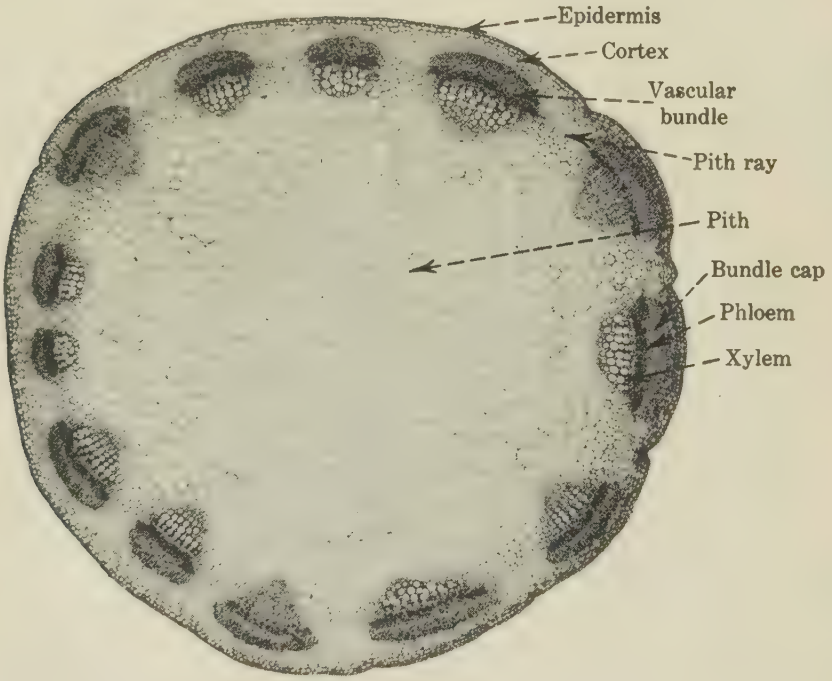


FIG. 25. Photomicrograph of a cross section of the stem of clover (*Trifolium repens*), an herbaceous, dicotyledonous plant.

since its cells continue to divide, and so are always meristematic, is not included among the permanent tissues.

In the mature region of the stem, differentiation of the primary permanent tissues is complete. These tissues may be summarized as follows:

PRIMARY PERMANENT TISSUES OF THE STEM

1. The epidermis.
2. The cortex.

3. The stele, including:
   (*a*) Pericycle.
   (*b*) Vascular tissue consisting of phloem and xylem.
   (*c*) Pith rays, if they are present.
   (*d*) Pith or medulla.

The Epidermis.—This is a single layer, the cells of which are generally isodiametric as seen in transverse section but somewhat elongated in the direction of the stem's length. The outer walls

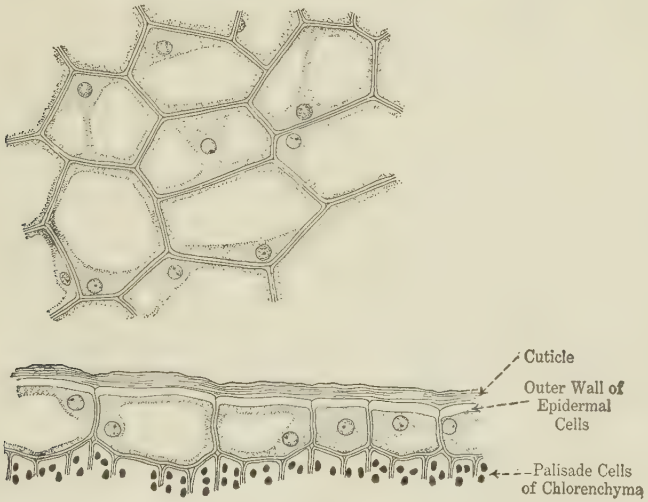


FIG. 26. Ordinary epidermal cells from the upper side of a leaf. Above, surface view; below, as seen in section. For the stomata and guard cells see Figs. 83 and 84.

are usually thickened and convex, and the outermost part of these walls consists of **cutin**, a waxy substance highly impermeable to water and gases. This cutin forms a continuous surface layer called the **cuticle**. The epidermis protects underlying tissues from excessive water loss, from mechanical injury, and from attacks of insects and fungi. In the epidermal cells the protoplasm forms a thin layer lining the wall. The protoplasts remain alive for a long time.

The Cortex.—This tissue group lies between the epidermis and the pericycle. The outer cells of the cortex, those lying just beneath the epidermis, are usually **collenchyma**, a type of tissue which constitutes the first-formed mechanical or strengthening tissue

of the developing stem. The cells of this tissue are elongated in the direction of the stem's length and characteristically thickened at the corners. They are first formed in very young parts of the stems which are still growing in length, and they are capable of considerable elongation after they are formed. Their walls are of pure cellulose, and their protoplasts are long-lived.

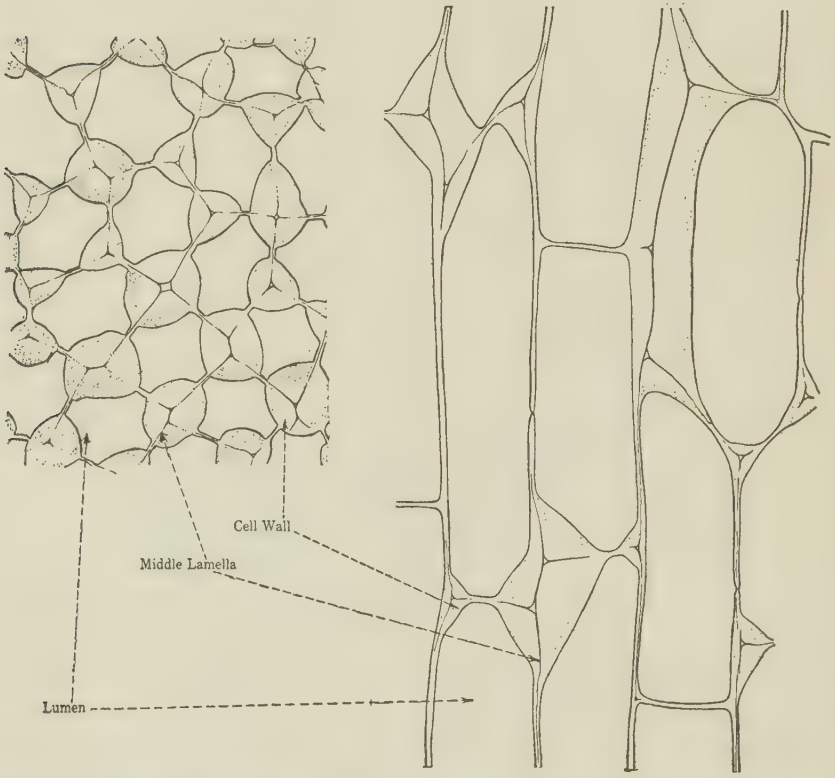


FIG. 27. Collenchyma tissue. (Left), cross section. (Right), longitudinal section. The cell contents are not shown.

Beneath the collenchyma is a zone composed chiefly of thin-walled parenchyma. Parenchyma tissue consists of large isodiametric cells with thin cellulose walls, large vacuoles, and with numerous intercellular spaces between them. The protoplasts of these cells remain alive for a long time. Parenchyma tissue is found in many different parts of the plant. Both the collenchyma and

parenchyma cells of the cortex frequently possess chloroplasts and consequently have the power of photosynthesis.

The Pericycle.—Internal to the cortex is the pericycle, a region which extends inward to the phloem. The pericycle is usually composed of two kinds of tissue—parenchyma, and a mechanical tissue composed chiefly of fibers. Fibers are elongated, thick-walled cells, generally pointed at the ends. Soon after fibers have attained their full size and thickness of walls the protoplasts die. The walls of fibers generally undergo lignification, that is, there becomes associated with the cellulose of the walls a substance known as lignin. This results in an increase in strength of the fibers but does not decrease their permeability to water and dissolved substances. Fibers are very elastic and can be stretched to a remarkable degree without losing their power to return to their original length. In the pericycle they may occur in separate groups or form a continuous ring.

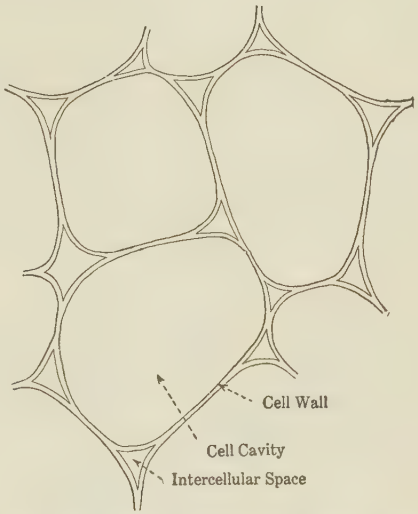


FIG. 28. Typical parenchyma tissue. The cell contents are not shown.

The Pith and Pith Rays.—The pith is made up of large-celled parenchyma with relatively numerous intercellular spaces. Its principal function is food storage. In stems in which the vascular tissue does not form a continuous hollow cylinder, the bundles are separated by pith rays, wide strips of parenchyma extending from the pith to the pericycle.

The Vascular Tissue.—The cells on the outer side of the procambium strands or cylinder become transformed into phloem and those on the inside into xylem. Some of the procambium cells lying between the xylem and phloem retain their power of dividing and constitute the cambium layer.

The Phloem.—The phloem of dicotyledonous plants generally consists of four kinds of tissue elements: sieve tubes, companion

cells, fibers, and phloem parenchyma cells. Sieve tubes are vertical rows of elongated cells, the end walls of which are thickened and provided with perforations (Fig. 29). Through these minute perfora-

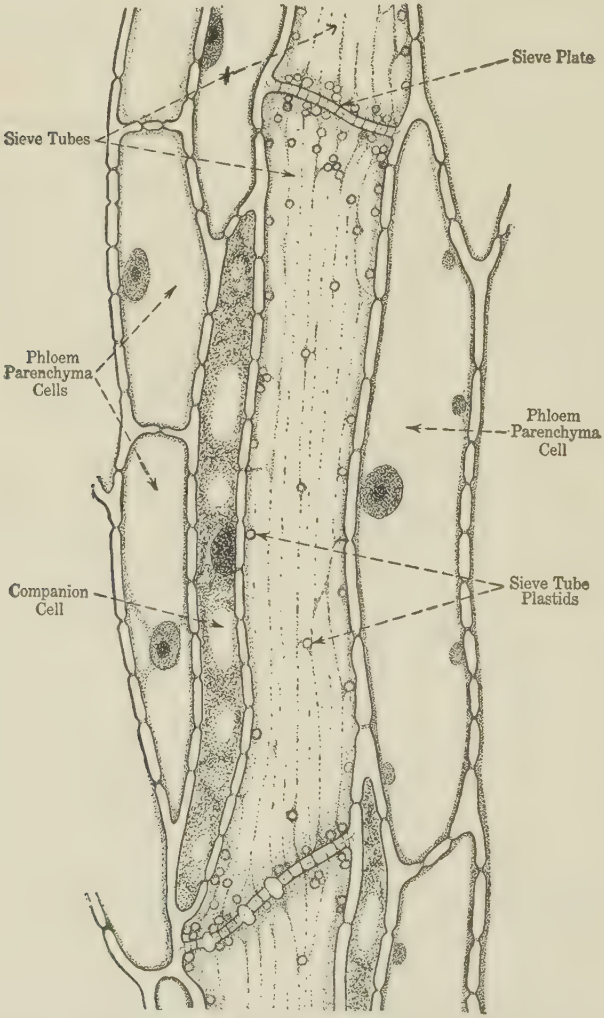


FIG. 29. Phloem tissue from the stem of *Nicotiana tabacum*, showing sieve tubes, companion cell, and phloem parenchyma cells. (Drawing, and section from which it was made, prepared by Crafts.)

tions (whence the name sieve tubes) pass cytoplasmic strands connecting the protoplasm of adjoining cells.

Nuclei are absent from mature sieve tubes, and the cytoplasm forms a thin layer surrounding a large central vacuole through which run lengthwise of the cells slender cytoplasmic strands. Adjacent to the sieve tubes there are generally found one or more parallel rows of elongated companion cells which may equal in length or are shorter than the cells composing the sieve tubes. They usually present a striking contrast to the sieve tubes by virtue of their small cross section, dense cytoplasm, and prominent nuclei. The walls of both companion cells and sieve tubes are of cellulose. Those separating the companion cells from the sieve tubes are generally perforated.

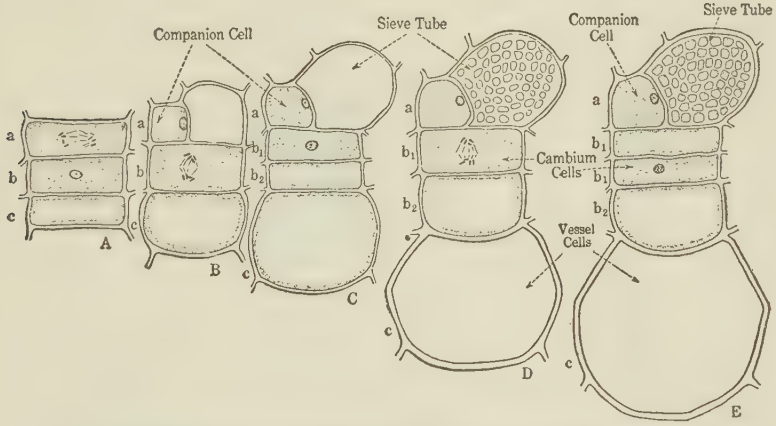


FIG. 30. Stages showing the differentiation of cambial cells. Diagrammatic.

It is probable that the principal function of phloem tissue is the longitudinal conduction of organic substances synthesized by the leaves. Since the sieve tube elements, as they mature, become permeable to all substances in molecular solution it is probable that they constitute the channels through which the organic substances move.

The Cambium.—This is a single layer of cells to which reference has already been made. It lies between the xylem and the phloem. Cambium cells retain the power of division, that is, remain meristematic. Cambium is made up of small, thin-walled cells flattened tangentially. Like all meristematic cells, they are rich in protoplasm. The cambium by tangential division of its cells gives rise to new phloem and xylem and thus causes increase in

thickness of the stem. Those cells which have recently been produced by division of the cambium layer differ little in appearance from the actual cambium cells.

Xylem.—The principal structural elements of the xylem are tracheids, vessels, xylem parenchyma, and xylem fibers. Tracheids are single cells which die soon after they are formed.

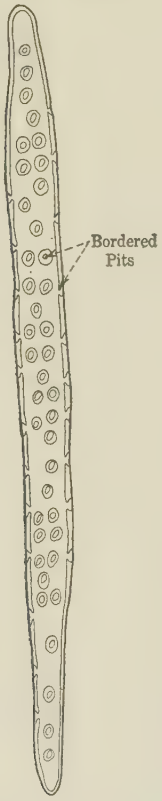


FIG. 31. A single pitted tracheid from pine (*Pinus*) wood.

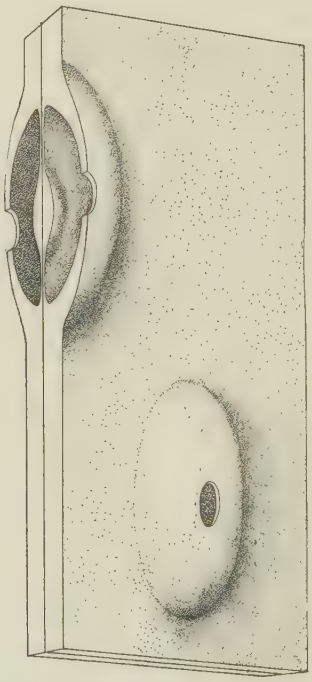


FIG. 32. Diagram showing the structure of a bordered pit. Above, the pit is shown in section.

They are always much longer than wide and are generally pointed at the ends (Fig. 31). The walls are thin in certain places and thick in others. Sometimes the thickening is restricted to rings or spiral bands running around the cells. In other cases the entire wall is thickened except for numerous small, round, or oval areas or pits (Fig. 32). The walls of tracheids are always lignified.

A vessel is not a single cell but a tube made up of a series of somewhat elongated, cylindrical cells with most of the cross walls dissolved away. By the time the vessels are ready to perform their function, the protoplasm of the component cells has died. These tubes, like the tracheids, have thickened areas in their walls. In young parts of the stem which have not yet finished growth in length, the thickened areas are in the form of rings or spirals. Those formed later, in a part of the stem which has finished elongation, have the wall much more completely thickened, the thin areas forming pits of various forms. The walls of vessels, as of tracheids, are always lignified. Vessels are often several centimeters in length (distance between two successive cross walls) and in some kinds of trees may be over a meter long.

Xylem parenchyma cells are short, thin-walled, and often pitted. Their protoplasts remain alive long after those of the vessels, tracheids, and xylem fibers are dead. They function chiefly as food-storage cells.

Xylem fibers are single, elongated cells, usually pointed at the ends, and with thick, lignified walls. They give strength to the stem.

We have spoken of pericyclic fibers, phloem fibers, and xylem fibers in the stem. Less common are epidermal and cortical fibers. Many of the plant fibers of commerce used in the textile industries are derived from some portion of the stem outside the xylem of the vascular bundles. For example, flax fibers, from which linen is made, are from the pericycle. Each fiber is a single elongated cell about one inch long. The wall is thick and of almost pure cellulose. Many cells are united in bundles which have a great tensile strength. Hemp fibers also develop in the pericycle. The hemp plant (*Cannabis sativa*) is extensively cultivated in both tropical and temperate regions. Jute is a fiber derived from the secondary phloem of two species of *Corchorus*, an Asiatic genus. Commercial fibers are also derived from "strands" in leaves and from surface hairs.

Gross Features of the Woody Type of Stem.—If we make a smooth cut across a woody stem, such as a several-year-old twig of cottonwood, apple, or pine, and examine it with a lens, we can see three distinct regions: the **bark**, the **wood**, and the **pith**. The bark, which includes the tissues outside of the woody cylinder, may be easily peeled away from the woody cylinder because of the layer of thin-walled, easily broken cambium cells lying next to

the wood. The cambium is such a thin layer of cells that it is not visible to the naked eye. The pith is seen at the center of the woody cylinder, and consists of soft parenchyma tissue. The woody cylinder is composed of a number of concentric rings, varying

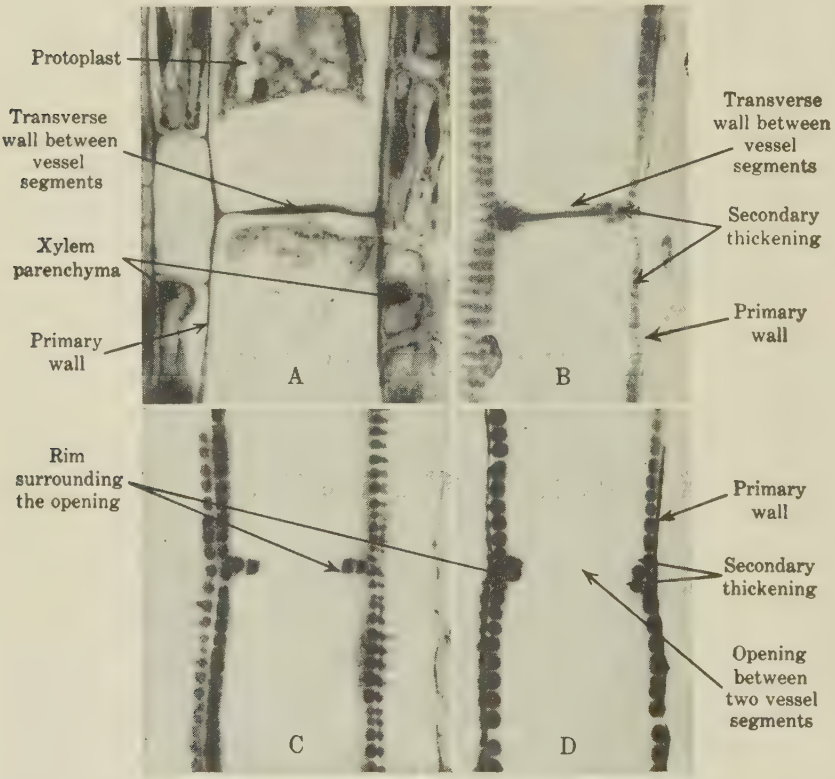


FIG. 33. Photomicrographs showing, in longitudinal section, development of spiral vessels in celery. *A*, the transverse wall between two vessel segments is intact; the segments contain protoplasts and their longitudinal walls are primary throughout. *B*, spiral secondary thickening has been laid down over the primary walls except over the central portion of the transverse wall. *C* and *D*, the central portion of the transverse wall has been dissolved away, the photoplasts have disappeared, and the vessel segments communicate with each other through a large opening. (From Esau.)

somewhat in width and known as annual rings. An annual ring consists of the tissue added by the cambium to the wood in a single year. The radiating lines seen in the wood also frequently extend into the narrow phloem region and are called vascular rays.

Internal Structure of One-year-old Woody Stem.—In the development of their tissues from the promeristem and the primary

meristems, woody stems are similar to herbaceous stems. The young portions of woody stems near the tip resemble the stems of the herbaceous type described above. The amount of vascular tissue is generally relatively less in herbaceous stems, and the pith and the cortex relatively greater in extent than in woody stems. The type of stem having distinct vascular bundles separated by pith rays and with interfascicular cambium between the bundles occurs somewhat less frequently among woody plants than it does among species with herbaceous stems. In some woody plants the vascular tissue is in separate bundles near the very tip of the stem but forms a hollow cylinder throughout the older part of the stem.

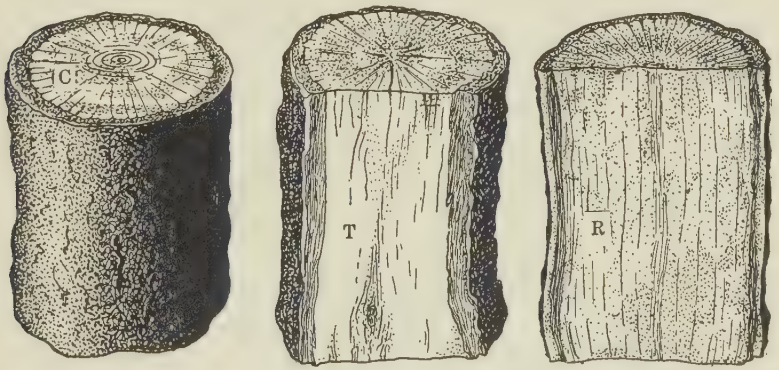


FIG. 34. Stems showing three kinds of sections: *C*, cross or transverse. *T*, tangential. *R*, radial.

Secondary Growth of the Woody Stem.—The changes from promeristem to primary meristems and then to the primary permanent tissues are spoken of as the **primary growth** of the stem. This growth ends when all the tissues have differentiated. The cambium is the only one of the tissues which remains meristematic throughout the life of the stem. By the time the primary growth has been completed, normally within a few months, growth in length of that part of the stem has ceased. Following this there is a secondary growth, resulting in an increase in the stem's thickness, which may continue for hundreds of years, or even several thousands in the sequoias. Secondary growth results from the production of new cells by two "lateral" meristems, the **cambium ring**, which has already been mentioned, and the **phellogen**, or cork cambium.

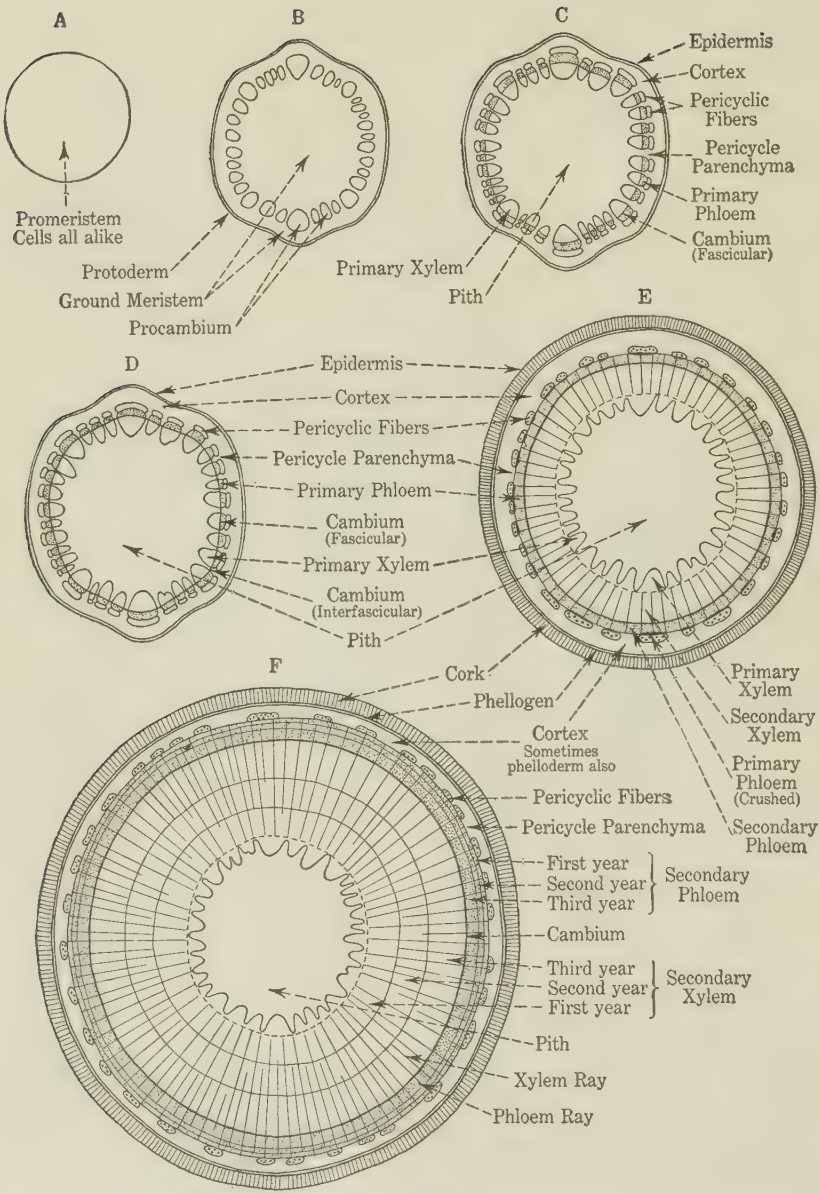


FIG. 35. Diagrams of cross sections of a dicotyledonous stem (*Sambucus*) showing primary and secondary growth up to three years. (Drawing, and section from which it was made, prepared by Esau.)

The Cambium Ring.—In stems with the vascular tissue (phloem and xylem) in a continuous cylinder the cambium is at this time already in the form of a continuous ring. In those having separate vascular bundles, the cambium is interrupted by the pith rays. In such cases, certain pith-ray cells lying between the cambium of adjoining bundles undergo cell division, giving rise to a row of rectangular meristematic cells similar to those of the bundle cam-

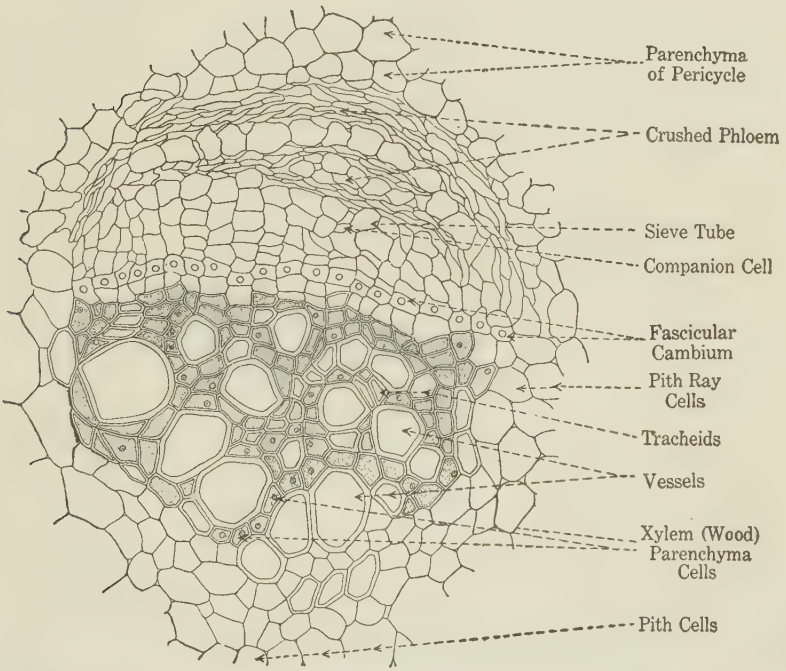


FIG. 36. Cross section of a young vascular bundle of a dicotyledonous stem. (*Aristolochia.*)

bium. This is known as the interfascicular cambium. Thus there is formed in these stems also a continuous cambium ring. This cambium produces new cells on the side toward the center of the stem and also on the outer side and thus causes radial growth of the pith rays.

The cambium ring in plants with a continuous vascular cylinder (most woody plants) by repeated tangential division of its cells gives rise to new xylem elements, new phloem elements, and new

vascular-ray cells which are radially elongated, long-lived, non-lignified cells which conduct materials radially. When a new xylem element is to be formed, a cambium cell divides tangentially into two daughter cells; the inner daughter cell, which is the one next to the xylem, develops into a xylem element, and the outer daughter cell, next to the phloem, remains a cambium cell. Then this cell, which has remained meristematic, again divides, and, generally, it

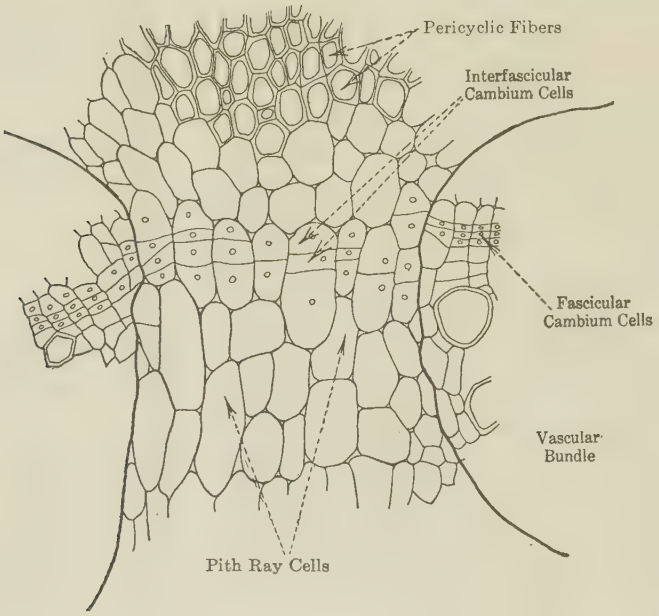


FIG. 37. Part of a pith ray and two vascular bundles of a young Aristolochia stem, showing the origin in the stem of interfascicular cambium cells from pith ray cells.

is again the outer daughter cell which retains its power of division, while the inner daughter cell develops into a xylem element. Less frequently, when a cambium cell divides into two daughter cells, the outer daughter cell, which is the one next to the phloem, develops into a phloem element and the inner daughter cell remains meristematic This process is repeated throughout the growing season. Thus by division of the cells of the cambium ring, a relatively large amount of new xylem is added on the outside of the old xylem, and a relatively small amount of new phloem is added on the inside of the previously formed phloem.

As the width of the xylem (from cambium ring to pith) increases, the distance between the phloem and the inner xylem becomes greater. As a result, there is need for better conduction of water radially from the xylem to the phloem and of food from the phloem to the xylem. This need is met by the production of vascular rays by the cambium. Here and there a longitudinal row of cambium cells or several adjoining rows cease the formation of xylem and phloem and produce radial rows of parenchymatous cells elongated radially, which constitute the vascular rays, spoken of as phloem rays in the phloem and xylem rays in the xylem.

The Cork Cambium or Phellogen.—When we use the term cambium or cambium ring it is understood that we are referring to the vascular cambium ring which lies between the xylem and the phloem, but in woody stems there is another cambium called the cork cambium. It usually arises in the cortex just below the epidermis, generally from a layer of collenchyma cells which become meristematic and by repeated tangential divisions produce daughter cells on both sides of the cork cambium. The outer daughter cells are transformed into cork cells. Such cells have walls impregnated with suberin which renders them very impermeable to water and gases. These cells die soon after they are formed. The inner daughter cells remain alive for some time and are more or less similar to the cells of the cortex. In the cork oak, cork cells are produced very abundantly and the "cork" remains attached to the trees for a number of years. From time to time it may be stripped off and put to commercial use in the manufacture of bottle corks, life preservers, etc.

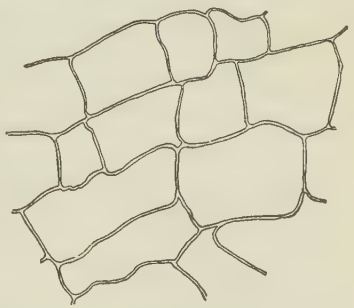


FIG. 38. Cork cells from the stem of Dutchman's pipe (*Aristolochia*).

As a protective tissue the cork replaces the epidermis when the latter tissue is no longer able to "cover" the stem which has increased greatly in circumference owing to secondary growth. It shields the tissues beneath from mechanical injury and from the entrance of insect and fungous parasites, and, because of its poor

conduction of heat, it protects the underlying tissues from sudden changes of temperature. Most important of all, as a waterproof covering, cork has no equal. It is because of this property that we utilize cork to close bottles containing liquids. The value of cork in checking water loss from the plant is well shown in the case of the potato tuber, which is covered by a thin layer of cork. It has been shown that a potato tuber with this layer of cork removed may lose in twenty-four hours over sixty times as much water as it did in the same period before it was "peeled."

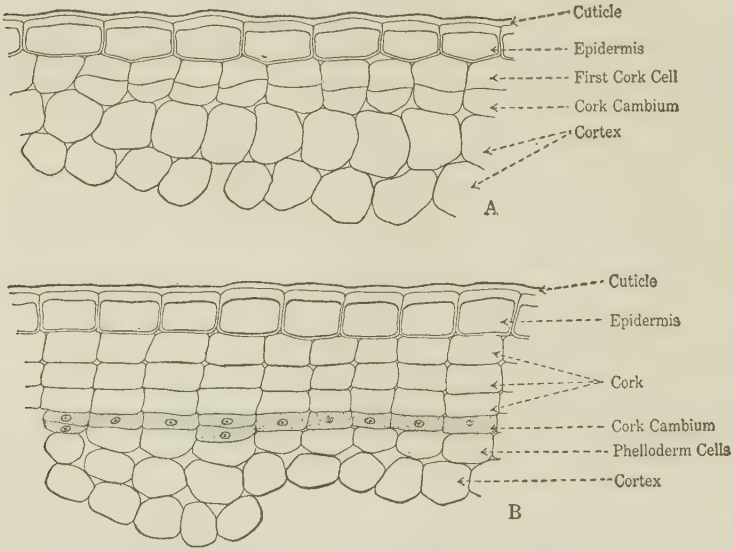


FIG. 39. Cross sections of portions of a stem showing origin of cork cambium (*A*), and the development of cork and phelloderm from cork cambium (*B*).

Lenticels.—Owing to the impervious nature of the cork layer formed beneath the epidermis of stems, access of oxygen to cells which underlie the cork would be practically impossible were it not for special ventilating regions in the cork called **lenticels**. They consist of groups of large, thin-walled cells, among which are many intercellular spaces. These cells arise from the cork cambium, and as they increase in number they finally break through the epidermis and project slightly above the surface of the stem. There is some loss of water vapor through the lenticels.

FIG. 40. Cross section of a young tree of cork oak (*Quercus suber*), showing the unusually thick bark produced by this species, which is the source of commercial cork. Such cork as is here shown, the so-called "virgin cork" is unsuitable for "corks." It is stripped from the tree by cutting almost to the cork cambium. The subsequently formed cork tissue is more compact and homogeneous and suitable for cutting into "corks." (Photograph furnished by the Division of Forestry of the University of California.)

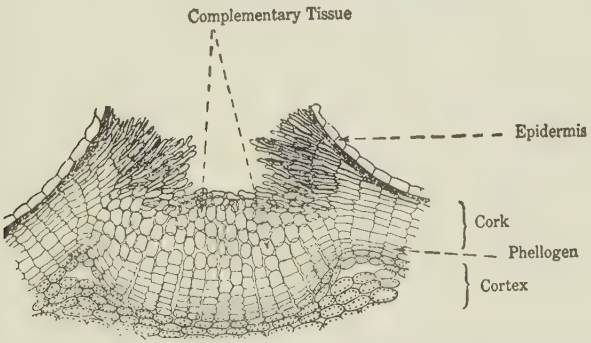


FIG. 41. Transverse section of lenticel of two-year old stem of elder. (*Sambucus nigra.*) (After Haberlandt.)

Annual Rings.—In temperate climates a season of cambial activity alternates with a period of inactivity. During each growing season a band of wood is produced by the cambium ring. As seen

FIG. 42. Cross section of a redwood (*Sequoia sempervirens*) log showing annual rings, light-colored sapwood, and dark-colored heartwood. Note the radial splitting which gives evidence of greater tangential than radial shrinkage of the cells during drying. (From Division of Forestry, College of Agriculture, of the University of California.)

on the end of a log, these layers appear as concentric rings. These are the annual rings to which reference has already been made.

Any one annual ring consists of two parts which are more or less readily distinguishable. These are the inner or spring wood and the outer or summer wood. The summer wood of one year

(1931, for example) adjoins the spring wood of the following year (1932). Hence, small, thick-walled elements of the summer growth of one year are adjacent to the relatively large, thin-walled wood elements of the spring growth of the following year, and the sharp line of demarcation between them is visible even to the naked eye (Figs. 42 and 43).

In general the annual rings produced during the first few years of the life of the tree are thicker than those produced later. Not infrequently a ring is distinctly thicker or thinner than the ring

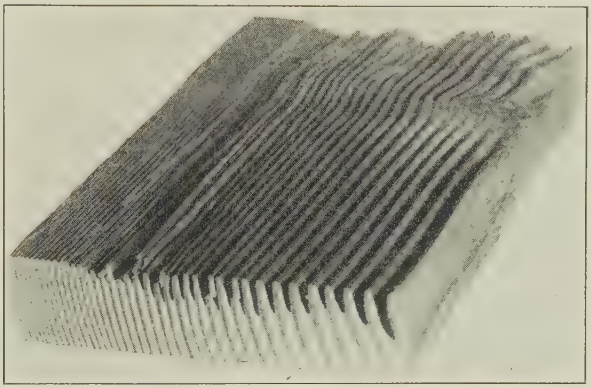


FIG. 43. Piece of a board of *Pseudotsuga taxifolia* cut from a saw guard in a lumber mill. Constant pelting with sawdust from the band saw has worn away the spring wood and left the thick walled summer wood almost intact. (Photograph furnished by Emanuel Fritz.)

produced in the previous or succeeding year. This variation is due to differences in light, heat, moisture, or other external conditions during different growing seasons. If we were able to interpret these variations, we would find that much of the history of a tree is recorded in its cross section. A study of the annual rings of very old trees has told us much of the climatic conditions long before man began to keep any records.

Determining the Age of Trees.—By determining the age of trees, employing either those that have been felled, or "cores" cut from standing trees by means of a hollow auger, the forester is able to ascertain the rate of growth of our important timber species and thus to estimate more accurately the annual increment of standing timber. This makes possible more intelligent practice

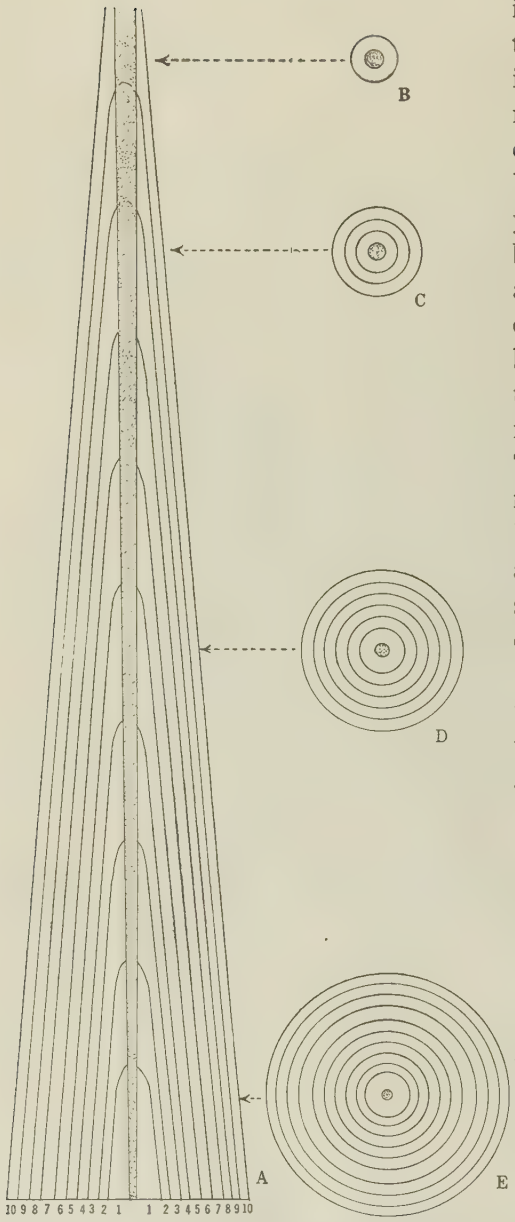


FIG. 44. Diagrams of longitudinal and cross sections of a ten-year-old tree. Note the decrease in the number of annual rings from the base of the trunk to the apex.

in the handling of our timber resources, including the annual cut permissible and the amount of replacement necessary. We have seen that each year a tree adds a new band of wood, called an annual ring, and that because of the difference between the spring and the summer wood these rings are clearly marked. The number of annual rings decreases from the base of the trunk to its apex, for near the tip the stem is only a few years old.

Wood. — We have used the term wood for the xylem part of trees and shrubs. From the forester's or lumberman's standpoint, wood is any part of the stem exclusive of the bark (tissue outside of cambium). Let us study the structure of the wood of an old dicotyledonous stem (trunk) by an examination of cross, radial, and tangential sections.

Cross Section. — In cross section, the annual rings appear as more or less parallel bands, each

with spring and summer wood. The wood rays are seen as narrow radial lines crossing the annual rings at right angles. The vessels,

FIG. 43. A cross section of the trunk of a relatively young tree of *Sequoia gigantea* (Big tree). The chalk lines and the arrows, except the central one, indicate approximately the annual rings formed in the years during which a number of events of great historic importance took place. The tree from which the section was cut began its growth in about A.D. 923 and was about 1000 years old when cut. There are trees now standing which are certainly twice that age and probably living trees 3000 years old exist.

tracheids, wood fibers, and wood parenchyma cells have their long axes running longitudinally, and accordingly in cross section the cav-

ities of the vessels appear as large, rounded pores: the tracheids and wood fibers are seen as much smaller and thicker-walled elements which are polygonal or square in shape: the wood parenchyma cells

FIG. 46. Joshua Tree, *Yucca brevifolia*. This and several other arborescent genera of the Lily Family are exceptions to the general statement that monocotyledons do not have a cambium layer and are without secondary growth in stem thickness. The cambium layer does not however produce new xylem on the inside and new phloem on the outside but produces on the inner side a succession of new "closed" bundles of relative small size and each containing both xylem and phloem tissue. Joshua Trees grow extensively in many desert localities in the Southwestern States. Unusually large specimens may have a trunk diameter of 5 feet at shoulder height and attain a height of almost 50 feet.

resemble wood fibers and tracheids in cross section but have thinner walls. Vessels, wood fibers, and wood parenchyma are absent from the wood of pine, spruce, and other gymnosperm woods.

Radial Section.—The annual rings appear in radial section as more or less parallel bands which impart to the wood its characteristic grain. Wood rays, as seen in radial section, appear as bands or bars of varying width and length, running at right angles to the vessels, tracheids, and wood fibers. Vessels appear as long, narrow grooves.

Tangential Section.—In tangential section, the annual rings appear as wide bands which may form various irregular figures.

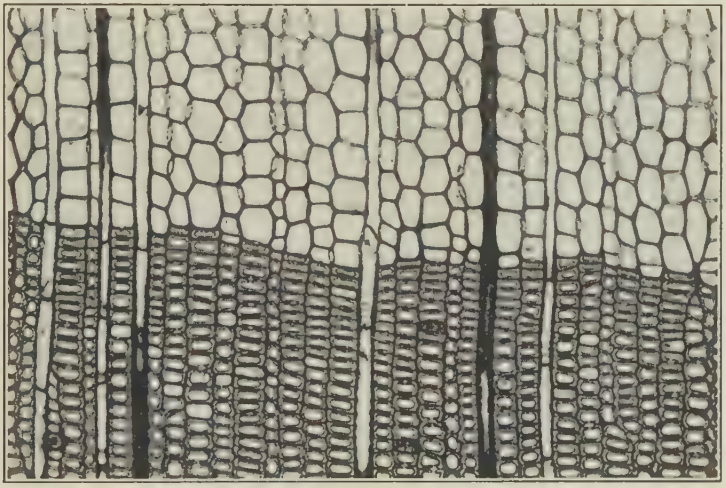


FIG. 47. Cross section of a portion of the wood of *Sequoia*. Portions of two adjacent annual rings are shown. Note the small, thick-walled tracheids of "summer wood," and the larger, and thinner-walled tracheids of "spring wood." (Photograph furnished by E. Artschwager.)

The wood rays are cut across and appear as lens-shaped groups of cells. Vessels, wood fibers, tracheids, and wood parenchyma appear much as they do in radial section.

Heartwood and Sapwood.—If we examine the cut end of a log, we observe that the woody cylinder consists of a light-colored outer zone, the **sapwood**, surrounding a dark-colored zone, the **heartwood**. Sapwood is composed of elements some of which, chiefly the wood parenchyma cells, are still alive, whereas heartwood consists of elements all of which are dead. The darker color of heartwood of most trees is largely due to the deposition in the cell walls and cell cavities of resins, gums, tannin, certain pigments, and

other substances. Transport of sap is almost entirely confined to the sapwood because the heartwood has undergone certain changes which prevent conduction of water through it.

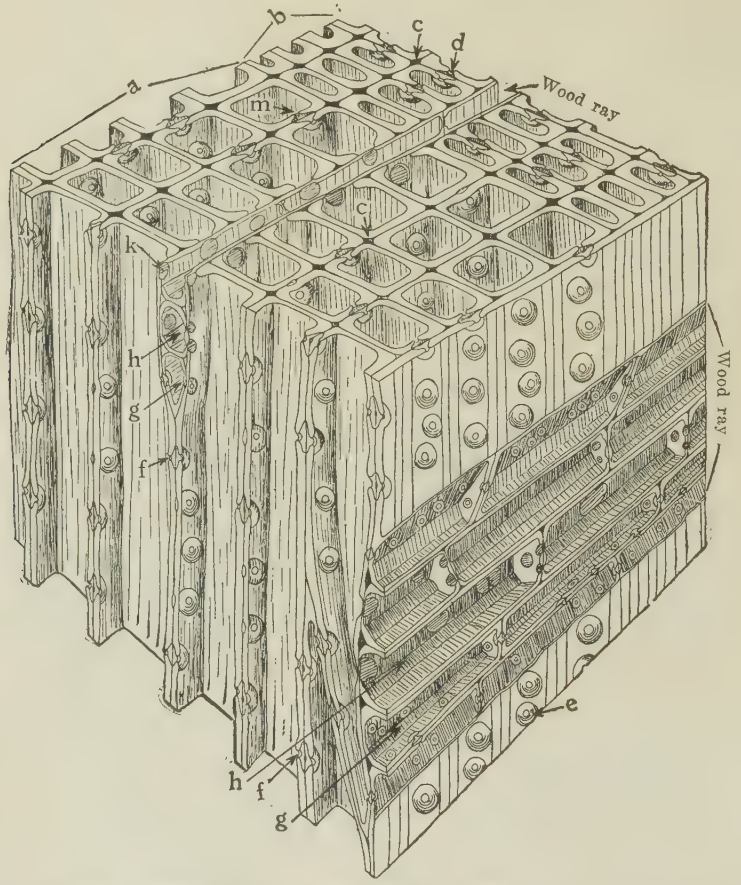


FIG. 48. Diagram showing block of pine wood. *a*, spring wood; *b*, summer wood; *c*, intercellular space; *d*, bordered pit in tangential wall of summer wood; *m*, *f*, and *e*, bordered pits in radial wall of spring wood; *h* and *g*, wood ray cells; *k*, thin place in radial wall of wood ray cell. (After Stevens.)

THE MONOCOTYLEDON TYPE OF STEM

The structure of monocotyledonous stems is very different from that of the stems which we have already discussed. This is clear from an examination of the corn stalk, which is a familiar example of a monocotyledonous stem. The phloem and xylem occur in

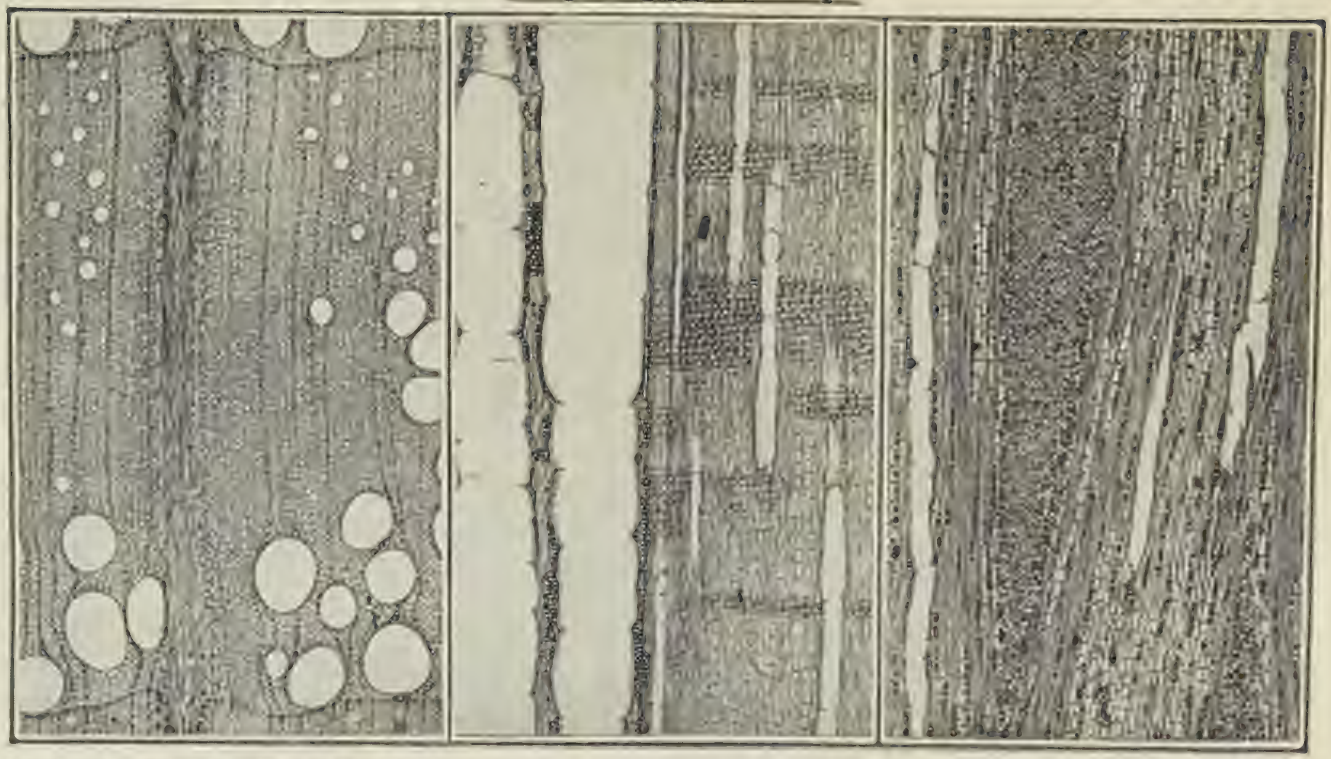


FIG. 69. Cross (left), radial (middle), and tangential (right) sections of the wood of red oak (*Quercus rubra*). Photographs by United Forest Products Laboratory, Madison, Wis.)

vascular bundles which do not form a definite vascular ring, as in dicotyledonous stems, but are scattered (Fig. 50). Moreover, the vascular bundles do not possess a cambium, for all the procambium cells are transformed into permanent tissues.

There is no distinct demarcation between cortex and pericycle in most monocotyledonous stems. Moreover, since the numerous vascular bundles are scattered through the stem, these stems lack a definite pith.

Owing to the absence of a cambium, monocotyledonous stems in general are not able to add to the quantity of xylem and phloem nor to increase to any considerable extent the number of cells in any of the other tissues. Therefore, such stems do not become much thicker as they grow older. Whatever slight increase in thickness does take place is the result of the enlargement of cells produced near the growing point. Whereas in the stems of perennial dicotyledons and gymnosperms, conducting elements of the xylem and phloem may cease to function within a few years, and are replaced by younger conducting elements, in perennial monocotyledons these elements retain their ability to transport materials throughout the life of the plant.

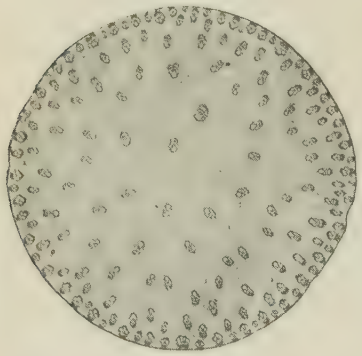


FIG. 50. Photomicrograph of a cross section through an internode of a stem of *Zea mays*, an herbaceous monocotyledonous plant. Note the many separate vascular bundles scattered through the parenchyma.

The stems of grasses are usually cylindrical in shape, and when mature their internodes are generally hollow, although sometimes, as in corn, they are solid. In many grasses the tissue at the very base of an internode remains soft and meristematic long after the rest of the internode has become matured.

FUNCTIONS OF STEMS

The primary functions of the stem are support of the leaves and conduction of water and raw materials for food manufacture to the leaves, and of food from the leaves. Secondary functions,

that is, those functions which the stem may carry on but which are at least equally characteristic of other organs, are food storage and food manufacture.

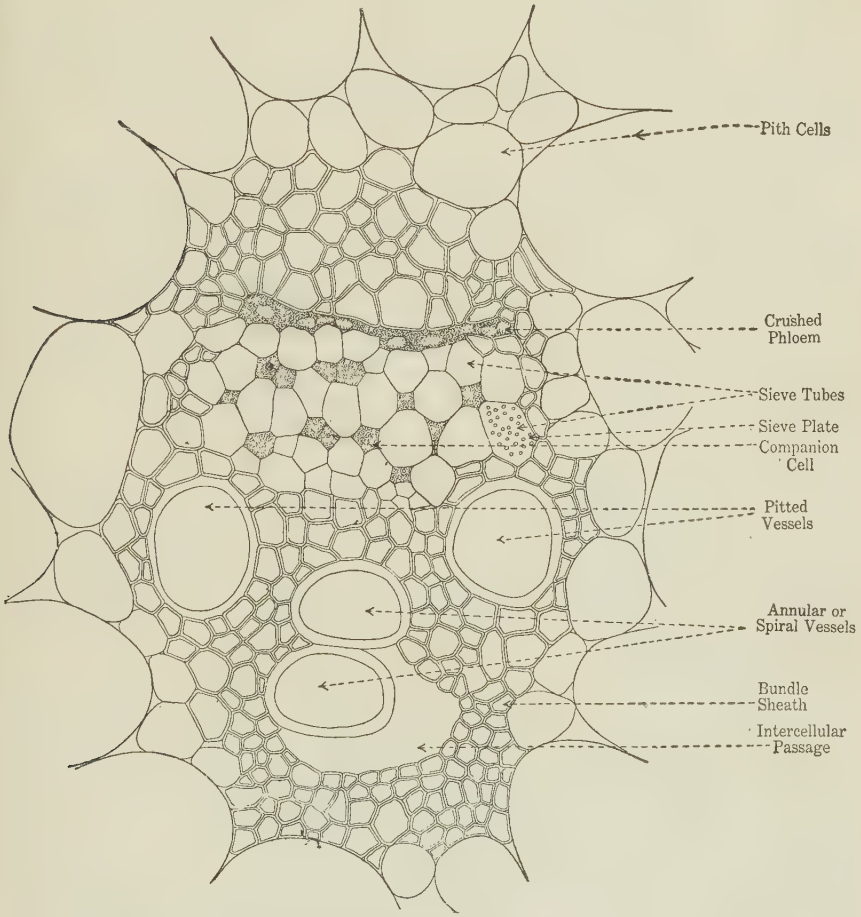


FIG. 51. Cross section of a vascular bundle of the stem of corn (*Zea mays*)—a monocotyledon.

Support.—The stem supports the leaves and so distributes them through space that they are in positions suitable for the absorption of light and thus conducive to photosynthesis. The elevation of the flowers on the stem favors both the transfer of pollen by wind and by insects and the dissemination of seeds.

Conduction.—The stem conducts (*a*) water absorbed by the roots from the soil, (*b*) dissolved inorganic substances also taken up from the soil by roots, and (*c*) various foods manufactured in the plant. In flowering plants the vessels are the chief carriers of water and inorganic salts from the roots to the leaves. This function is shared to some extent, however, with the tracheids; and in pines, spruces, firs, and other gymnosperms, which lack vessels, tracheids are the only elements for conduction of water and inorganic salts longitudinally.

The rate of movement and the path of water and inorganic salts up the stem may be roughly ascertained by placing a leafy branch, which has been cut under water, in a solution of eosin, indigo, carmine, or any one of various other dyes. After a short time a series of cross sections at different elevations or a longitudinal section of the stem will show the presence of the solution only in vessels and tracheids, and also the height to which the solution has risen since the stem was placed in it.

Destroying the pith and the tissues outside the woody cylinder (phloem, pericycle, cortex, and cork or epidermis) does not interfere with the upward conduction of water and solutes. Lateral transfer of these from the wood to the other tissues of the stem is probably by means of wood parenchyma cells, vascular rays, and pith rays when they are present.

Although complete girdling of a tree, that is, the removal of a ring of bark of the trunk, does not shut off the upward movement of water, the downward movement of foods is interfered with, and the tree finally dies. This probably results from the rather prompt death of the roots, because of their inability to get food. The girdling of stems often results in increased growth above the girdle; it is a common practice to girdle the stems of currants in order to increase the yield of fruit. In both cases the result is probably due to the girdle restricting the movement of food away from the upper part of the plant.

The Factors Responsible for the Rise of Sap in Stems.—The quantity of water which may be transpired from a tree in a single growing season and which must therefore be conducted up the stem during that time is astonishingly great. For example, it has been estimated that a hundred-year-old beech tree, bearing

perhaps a quarter of a million leaves, may lose in the period from June to November, inclusive, as much as 20,000 pounds of water. This water is often raised to great heights, as in the redwood (*Sequoia sempervirens*), and the question of how this water, and the small quantity of substances from the soil dissolved in it, is raised, has long been of very great interest.

There has been a tendency to attempt an explanation of this phenomenon on the basis of one simple mechanism, or at least a few interrelated functions. It now seems apparent that a number of processes are involved, the more important of which are (1) osmosis, (2) root pressure, (3) the functioning of living cells, (4) imbibition, (5) transpiration pull and water cohesion, and (6) capillarity. The part played by each of these will now be discussed.

1. *Osmosis.*—It was pointed out in the discussion on osmosis that water tends to flow in the plant from regions where water molecules are relatively abundant to regions where they are relatively few. The flow of water into root cells is along such a positive gradient of water. It appears, furthermore, that the movement into the xylem vessels occurs along a similar gradient, the relative concentration of water in these elements depending at some times upon the concentration of solutes in the xylem sap and at other times upon the hydrostatic pressure as affected by transpiration pull. In the transpiring leaves water again flows through living cells from the xylem to the exposed surfaces of mesophyll, from which it is finally evaporated. Wherever water moves through living cells in the plant its rate and direction of flow are determined by osmotic forces.

2. *Root Pressure.*—The movement of water attending rapid solute absorption by the roots of higher plants sets up in the xylem a pressure which is known as root pressure. This may be easily demonstrated by cutting off the main stem of a vigorously growing plant above the ground and replacing it with a glass tube attached by rubber tubing (Fig. 52). After some time, if conditions are right, sufficient water may enter the plant to raise the sap column to a height of several meters, and in extreme cases as high as 15 meters. Although such pressure will not explain the rise of sap to the top of tall trees, this mechanism is apparently present in all plants and affects the uptake of water. In plants abundantly supplied with water and having little or no water loss, it may be the principal

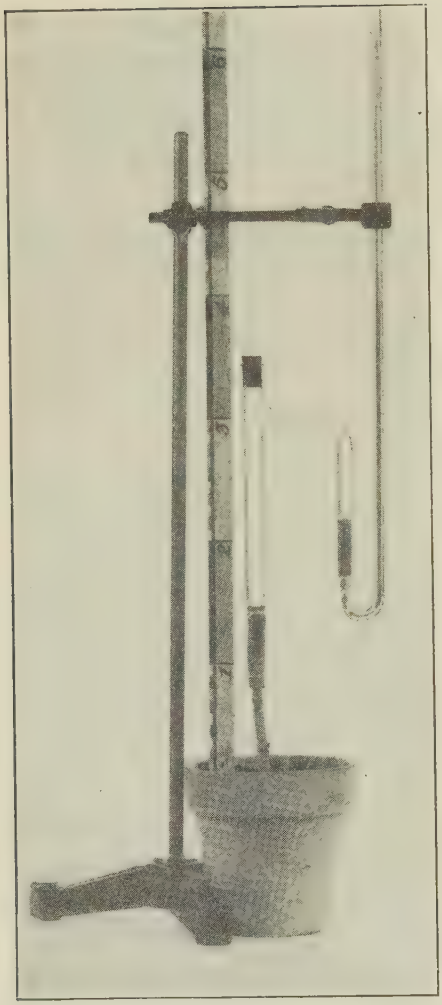


FIG. 52. Demonstration of root pressure. To the stump of the Fuchsia plant which grew in the pot, a glass manometer (device for measuring pressure) was attached by rubber tubing. As shown in the figure the manometer was filled partly with water and partly with mercury. At the beginning of the experiment the level of the mercury was the same in the two arms of the U-tube. As root pressure developed the mercury was forced upward in the right arm of the U-tube, which was open at the top. The level of the mercury in this arm rose 40 cm. above that in the other arm, showing a root pressure sufficient to raise water to a height of over 5 meters, or about 16 feet.

factor in water movement. It is an osmotic mechanism, however, and slow in its action, especially when approaching its limiting activity. In the functioning plant root pressure is of minor importance in water movement once transpiration becomes active, and when water loss reaches excessive proportions the very structure that makes root pressure possible may hinder water absorption and result in dangerous water deficits within living tissues. The root-pressure mechanism becomes totally ineffective when available moisture becomes low in the soil.

3. *Functioning of Living Cells.* — Although the theory that living cells exert a pumping force upon the water in xylem vessels has been abandoned, experiments in which the xylem is injured show that eventually vessels in the injured region become plugged with gummy substances or blocked with air bubbles. It seems essential that the conducting elements in the xylem be associated with living cells in order to maintain a condition favorable to their functioning. The reason for this will be apparent in the discussion of water cohesion.

4. *Imbibition.* — The per-

meability of cell walls and cytoplasm to water, the maintenance of structure within the plant, and the provision of moist surfaces for gas absorption seem dependent upon imbibition by colloidal substances. It seems doubtful if the functions of water absorption, water movement, and water loss could be carried on by the plant were it not for imbibition of water by plant membranes.

5. *Transpiration Pull and Water Cohesion.*—With the evaporation of water from mesophyll cells and the concentration of solutes in the cell, sap water is withdrawn osmotically from the tracheids in the veinlets of leaves. Accordingly, a pull is exerted on the upper end of the water columns in the conducting elements and the entire sap stream is raised. This requires that the sap columns from the leaves to the roots be continuous and that these sap columns have sufficient tensile strength to prevent them from breaking. Experiments using both water and plant sap indicate that these requirements may be met. There seems to be no question that the cohesion (resistance to breaking under tension) of water within the narrow tubes is more than sufficient to transmit the tension (pull) throughout the entire length of the columns without breaking. The cross walls in the vessels and the end walls of the tracheids do not prevent the movement of sap, for these walls are saturated with sap and movement takes place freely. It was formerly believed that bubbles are of frequent occurrence in the conducting elements of the wood, which interfere with the flow of sap, but it has been shown that in intact stems the conducting tracheids and vessels of the sapwood (through which the movement of the sap takes place) contain no bubbles.

It should be realized that the sap under tension in the tops of tall trees, and even in the roots when transpiration is high and soil moisture deficient, exists in an unstable condition and would immediately go over into vapor if conditions were right. However, for the vapor phase to be initiated, it is apparently necessary that some surface not perfectly wet be present upon which the first bubble can originate. This movement of sap under high tension in plants seems to depend upon the fact that all structures inside the system of xylem vessels and tracheids are thoroughly wet by the sap and no opportunity is afforded for the formation of the vapor phase. It is interesting that in order to stay in this perfect condition the conducting elements

must exist in living tissues and be associated with living cells. Movement of sap under tension through killed xylem soon ceases because of the formation of bubbles, and the mechanism becomes inoperative.

6. *Capillarity.*—The force of capillarity affects the movement of sap in the xylem in at least two different ways. First, the ultimate movement of water molecules into the atmosphere from the moist surfaces of mesophyll cells causes a deficit in the imbibed water of the walls of these cells. This results in the recession of the film from the wall surface into the molecular interstices of the cellulose of which the wall is made. Consequently capillaries are formed that are of molecular dimensions and capable of exerting extreme forces upon the water. This is apparently the mechanism responsible for the development of the immense force required to lift sap to the tops of the highest trees.

The second application of capillarity is in the disappearance of bubbles formed during times of extreme stress in the tensile sap columns of the xylem. When a bubble is formed in a vessel or tracheid, the two opposed menisci at its two ends tend to press on the vapor and collapse it. Opposed to this is the pull on the sap columns that has formed the bubble. If the tension on the sap is decreased by reduced transpiration, increased water absorption, or both, the force of capillarity remaining unchanged may exceed the lowered tension and when this occurs the menisci approach each other, press the vapor back into solution, and the bubble disappears. Thus the conducting elements of the xylem may be returned to a functioning condition after bubbles have formed in them if the tension of the sap in them becomes sufficiently reduced. This phenomenon can be produced artificially in the xylem elements of certain stems and the whole process of bubble formation and collapse observed under the microscope.

It is apparent from this discussion that a number of functions are involved in the mechanism of sap movement in the xylem. While this mechanism might conceivably function without the aid of living cells, experiments have shown that it is so delicately adjusted to the structural arrangement and to the extreme forces involved that almost any disturbance will upset it and render it ineffective. The principal part played by the living cells is ap-

parently one of maintaining the vessels and tracheids in a functioning condition, free from obstructions and from contaminated surfaces upon which bubbles could form.

Conduction of Food.—Carbohydrate (sugar and starch) formation takes place in green portions of the plant, principally in the leaves. Some protein is formed in the leaves also. Food produced in the leaves is constantly being carried away into the stems and through the stems to various parts of the plant, where it is stored or used for the formation of the protoplasm of new cells at the growing points of roots and stems or in the cambium region. However, before starch and protein can move out of the leaves they must be changed into simple substances (sugars and soluble organic nitrogen compounds) which are soluble and can pass from cell to cell. These may be changed back into starch and protein in the storage tissues.

Downward conduction of foods takes place chiefly in the phloem of the stem. It is known that complete girdling (or ringing) of the trunk of a tree by removal of a band of bark to the depth of the xylem, all the way around the stem, eventually results in the death of the tree through starvation of the roots. Chemical studies on the composition and especially on the changes and gradients in soluble foods in the phloem indicate that movement of these materials takes place through phloem tissues and that concentration gradients are involved in the rate and direction of movement. The rate at which food moves downward is much too rapid to be explained by mere diffusion and at present no completely satisfactory explanation of this transfer of food in the phloem has been proposed.

Foods may also pass transversely in the stem along the vascular rays. The rate of such movement is relatively slow and may be explained by diffusion accelerated by protoplasmic streaming in the ray cells. Conducting elements of both phloem and xylem come in intimate contact with vascular-ray cells. Thus the vascular rays are able to carry food from sieve tubes radially into the cambium and xylem, where it serves to thicken the walls of developing xylem elements and to supply the needs of the protoplasts of living cells. This lateral movement also provides an abundance of food materials to the phloem, xylem, and pith for storage against future needs.

FIG. 53. Demonstration of transpiration pull (water-lifting power of transpiring leaves). A leafy shoot, cut off under water, is fastened (water-tight) into a perpendicular tube filled with water and with its lower end dipping into a vessel of mercury. As the transpiring shoot withdraws water from the glass tube, mercury is drawn upward into the tube. The height of the mercury column at the time the photograph was made was 27 cm., equivalent to a water column of more than 3½ meters or about 11½ feet. It is possible thus to raise mercury to a much greater height.

Storage in Stems.—Various substances, such as water, food, and waste products, may accumulate in stems. These stored products may or may not be utilized later by the plant. The fleshy stems of such plants as cacti or begonia accumulate large quantities of water in the cells of the cortex or pith. In certain cacti so much water is thus stored that travelers in desert regions where such plants grow sometimes use the plants as an emergency source of drinking water.

Stems may also serve as storage places for food. Subterranean stems, such as tubers, rhizomes, and corms, are especially adapted for this. Starch is the most common form of food stored in stems, but cane sugar (sucrose), reserve fats, and proteins are also present. The starch is formed within the leucoplasts of the storage cells when surplus sugar (probably glucose) reaches these cells from the leaves. Before the reserve carbohydrate can leave the storage organ to be used elsewhere in the plant, it must be digested to form sugars again.

The stems of some plants accumulate such substances as mucilage, resins, essential oils, tannins, and latex, the plant material from which rubber is produced. Most conifers produce **resin**, an important commercial product, in "resin ducts" in their stems. The best-known resin is common rosin produced in our southern states, and derived from several species of pine. Turpentine or spirits of turpentine is a volatile substance obtained by distillation of the exudate of pines. **Tannins** are found in the stems of many plants. They are particularly abundant in the bark of tan oaks, and in the heartwood of many trees. **Latex** is a milky secretion, an oil-in-water emulsion, formed in the highly branched system of tubes without cross walls which extend throughout certain plants. Latex occurs in many different plants such as fig, milkweed, euphorbia and dandelion, and the rubber plant (*Hevea*). The very important part which rubber plays in modern commerce, particularly in connection with the electrical and automobile industries, has directed a great deal of attention to latex and latex-producing plants, for the latex is the principal raw material of rubber. The most important rubber-producing species is *Hevea brasiliensis*, but a number of other members of the spurge family and the fig family are of some importance as sources of rubber. The substance gutta-percha is

derived from the milky juice of *Palaquium oblongifolia,* and others of the same genus, native of the East Indies and the Malay Peninsula.

Propagation by Means of Stems.—It is a familiar fact that many plants may be propagated (multiplied) by means of "cuttings" or stem pieces. When these cuttings are placed in moist soil, roots develop at the lower end, and one or more axillary buds at the upper end develop into leafy shoots. Thus, each cutting grows into an independent plant. Under natural conditions, pieces of the stem may become detached and develop in the same way into new plants. Propagation by means of cuttings, whether of stems or of other vegetative structures, is of great importance in agriculture, because by this method new plants may be secured which are true to type, whereas many species of agricultural plants when propagated by seeds produce plants quite different from the parents. Propagation by means of cuttings of stems, roots, or leaves, or by grafting, often has the additional advantage that the cuttings or grafts develop more rapidly than plants grown from seeds.

Many plant cuttings, which ordinarily will not root at all or only with some difficulty, form vigorous roots when treated with certain chemical compounds, the common one used commercially being indoleacetic acid (heteroauxin). For example, lemon cuttings were smeared with a paste containing one part of pure synthetic indoleacetic acid mixed with 2000 parts of pure lanolin, and their behavior compared with untreated cuttings. Root formation was stimulated by the treatment. Although indoleacetic acid is one of the most common root-stimulating substances, experiments have demonstrated the existence of sixteen or more substances which induce initiation of adventitious roots.

Vitamin B_1 has become another common growth-promoting substance. Whereas the auxin influences root initiation, vitamin B_1 influences root growth. If treatment of cuttings with the auxin fails to give results, in many cases a subsequent treatment with vitamin B_1 meets with success. The concentrations used are, for indoleacetic acid, from 1 part in 5000 to 1 part in 40,000 water; for vitamin B_1, 1 part in 1,000,000 water. In commercial practice the cuttings to be treated are simply immersed for a period in water containing the extremely small concentrations of the growth substances.

These growth-promoting or growth-stimulating substances are known to be produced by a considerable variety of plants. They

have also been extracted from animal sources. They are organic substances, and, although they occur in very minute quantities, they are capable of producing marked physiological effects. In addition to their influence on root production, there is reason to believe they may affect respiration, dominance of certain parts of plants over others, flower production, fruit formation, elongation of cells, and plant movements. Their rôle in cell enlargement and certain tropisms was discussed on page 23.

FIG. 54. Iris plants showing the rhizomes with leafy shoots and roots. (From Bocquillon.)

Certain of these substances (auxins) are present in many seeds; in some the amount decreases rapidly during the early germination stages. In other seeds, such as oats, no auxin occurs in the dry seed but rapidly appears in the endosperm when it absorbs water. Some seeds but not all, when treated for a short time with an auxin, may have their percentage of germination increased, and the subsequent growth may be more rapid than that from untreated seeds. Auxins are also produced in growing buds and in young leaves; in the latter organs its formation is dependent upon illumination. Although auxin is present

in roots, there is some uncertainty as to whether or not it is actually formed in them.

It appears that vitamin B_1 is a general growth factor for the roots of higher plants. It is formed in green leaves in the light and stored in seeds. It is of interest to note that organic manure contains appreciable amounts of vitamin B_1, which suggests that the beneficial effects of manure may be due in part to the presence of this substance.

It has been shown that the growth of many species of plants is promoted by slight additions of vitamin B_1 to the soil in which the plants are grown. This vitamin is manufactured in green leaves, and there is evidence that at times the amount manufactured may not be sufficient to give the best root development. This is particularly the case with cuttings, which may have no or little leaf surface, in which root production may be stimulated by additions of vitamin B_1. Some plants, tomatoes and wheat for example, do not respond to vitamin B_1, or other growth-promoting substances, at least under the cultural conditions employed in the tests; and it is assumed that these substances are produced in the plants in quantities sufficient to satisfy their needs.

Propagation by **grafting** is a very old horticultural practice, and is in common use in propagating fruit trees. In grafting, a piece of one stem, called the **scion,** is attached to another stem, which is rooted and is called the **stock,** in such a way as to bring together the cambium layers of each and cause the two to grow together. **Budding** is a horticultural practice which is essentially the same as grafting. It differs from grafting only in the character of the scion, the scion used being a single bud together with a small strip of adjoining bark which is inserted underneath the bark of the stock.

STEM MODIFICATIONS

Ordinarily we think of a stem as a cylindrical organ growing more or less erect. However, there are many modifications of stems differing so much in form and in other respects from the ordinary type that they are scarcely recognizable as stems, and careful study of their origin and structure is often necessary to identify them as such. Examples of these modified stems are rhizomes, tubers, bulbs, corms, runners, and tendrils.

Rhizomes (or rootstocks) are elongated, horizontal underground stems, generally rich in stored food. The rhizomes of Canada thistle, Johnson grass, quackgrass, wild morning glory, iris, and many ferns are good examples. Rhizomes generally produce large num-

bers of adventitious roots. Many of our most pernicious weeds are rhizome-bearing perennials. It is not enough to prevent the formation of seeds in these plants to eradicate the weeds. The plant is still capable of propagating itself readily, for if the rhizomes are broken into a number of separate pieces by cultivating implements,

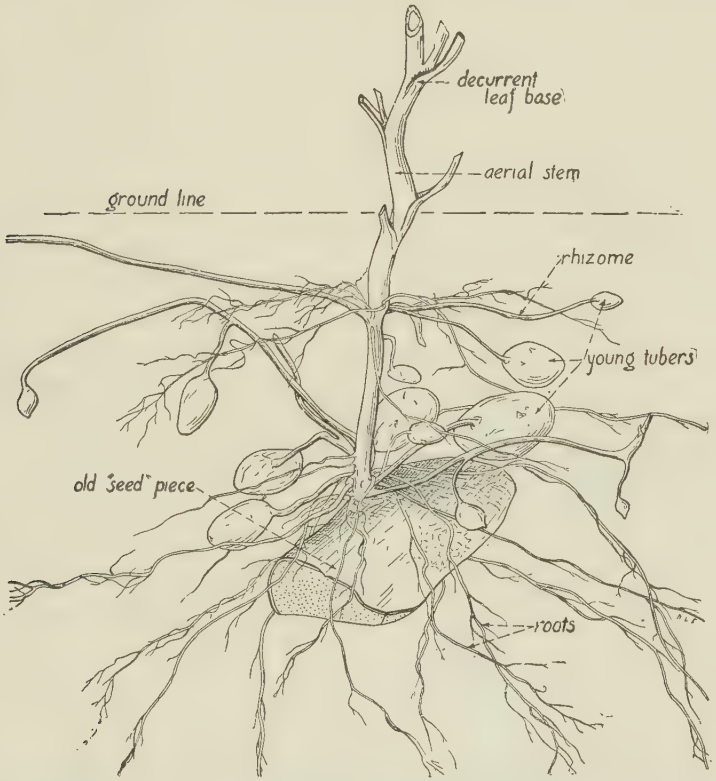


FIG. 55. Portion of a sprouting potato tuber. (After Robbins, *Botany of Crop Plants.*)

each piece may grow and send up green shoots. Since food is made only in the green parts of the plant above the ground, repeatedly cutting off the green shoots as soon as they appear above ground will finally kill the rhizome through the successive drains on its stored food.

The control and eradication of perennial weeds by chemicals (herbicides) is now a common practice in many agricultural sections. Within recent years thousands of acres of weed-infested lands in western United States have been

treated with herbicides. In the application of chemicals to destroy perennial weeds, the object is to bring toxic substances in contact with the roots and

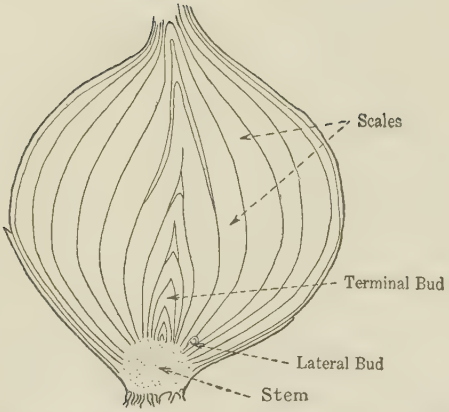


FIG. 56. Median longitudinal section of an onion bulb.

FIG. 57. Corm of crocus, in median longitudinal section. (Redrawn from Figurier.)

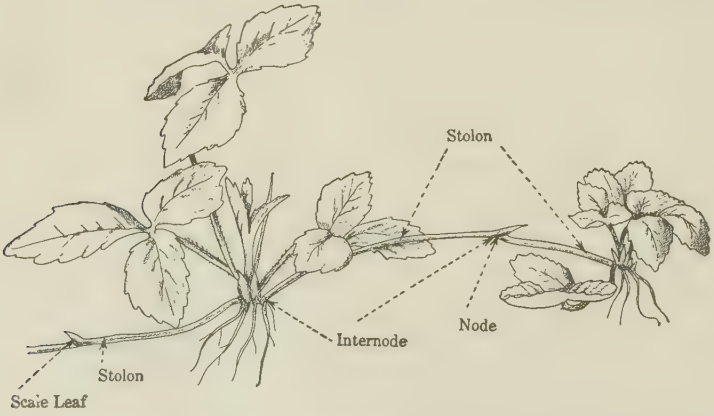


FIG. 58. A strawberry (*Fragaria*) plant showing propagation by means of stolons.

rhizomes, thus causing their death. The chief herbicides employed to kill deep-rooted perennial weeds are carbon bisulphide, chlorates (chiefly sodium

chlorate), borates, and certain arsenical compounds. Carbon bisulphide is a clear, water-like liquid which is highly volatile. When injected into the soil the volatile gas diffuses through the soil, killing roots and rhizomes with which it comes in contact. Chlorates and borates, applied as dry crystals or as a solution in water to the soil surface, are effective only if the chemical is carried into the soil by rain or by irrigation water to levels where it can be absorbed directly by the roots. Arsenical compounds, rendered acid, are applied as a spray to the foliage. If the weeds treated have a water deficit throughout their tissues, the spray material will enter the vessels of the leaves and stems, and be "sucked" downward into the roots and rhizomes. (See page 123 for a statement regarding the chemical extermination of annual weeds.)

The most familiar example of a **tuber** is the Irish potato. A tuber is a much-enlarged, short, fleshy underground stem, usually lacking roots, and produced at the ends of rhizomes. The potato plant may be propagated by planting the whole tuber, or by cutting it into pieces, each piece having one or more "eyes," which are groups of buds.

The **bulb**, a typical example of which is the onion, consists of a short, flattened underground stem, from which arise numerous fleshy scale-like leaves filled with stored food.

The **corm**, well exemplified in the crocus and gladiolus, is a short, solid, vertical, enlarged underground stem, usually flattened from top to bottom. It bears a cluster of thick, fibrous roots on the lower side, and a tuft of leaves on the upper.

The strawberry plant is illustrative of a plant bearing **runners** (or stolons). A runner is an elongated stem which grows horizontally along the surface of the ground, every here and there taking root and sending up a new shoot. The strawberry naturally propagates itself by means of such runners, for after the new shoots are established the runners connecting them die.

Occasionally stems are modified as **tendrils**, as in the fox grape, spines as in the honey locust, or leaf-like photosynthetic organs as in the cactus.

CHAPTER V

THE ROOT

Often, half, or more, of the total weight of a seed plant consists of roots, and the roots of a plant are often of very great number and extent. For example, the root system of a single corn plant at the stage where it has developed eight leaves may have 8000 to 10,000 lateral roots, arising from 15 to 23 main roots; the roots of the desert plant, *Yucca glauca,* have been found to extend horizontally a distance of 30 feet or more; and alfalfa roots may grow downward into the soil to a depth of 10 to 25 feet.

From the soil the roots absorb water and mineral salts, constituents used by the green plant in the manufacture of foods. The development, extent, and activities of roots are as influential in determining the normal growth of the plant as are the leaves or stems.

Within recent years much study has been devoted to the relation of roots to their soil environment, and especially to the root habits of crop plants as they affect crop production. There are marked differences among species and varieties in their ability to penetrate deeply into a soil with little water, or in their ability to penetrate impervious or poorly aerated soil. Cultural practices influence the character of the root system. For example, by an improper system of deep cultivation of corn in certain parts of the Corn Belt, it is estimated that, as a result of root injury, the yield of corn was decreased 2 to 8 bushels per acre. In this case, a study of the root habits of corn led to the adoption of proper tillage methods.

The root system responds to the soil environment. The most important of the factors influencing the general character and behavior of roots are moisture, supply of necessary salts in the soil, oxygen supply, and temperature and texture of the soil. As an example, root systems are usually more shallow in poorly aerated and wet soil than in well-aerated and moderately moist soil. More-

over, particularly at high soil temperatures, good aeration of the soil is necessary if normal root growth is to take place.

It is becoming recognized that a knowledge of the extent of the roots and their development and of their reaction to the conditions which surround them in the soil is essential to an intelligent application of tillage, transplanting methods, the distribution in the soil of water and fertilizers, and crop succession.

Kinds of Roots.—According to their origin, roots may be classified as **primary, secondary,** and **adventitious.** When a seed germinates, usually the first structure to make its appearance is the rudimentary root (**radicle**). This develops into the **primary root.** It is the first root of the plant and in many species (e.g., radish, beet, carrot) remains the principal one throughout the life of the plant. Its branches are called **secondary roots.** All roots which do not arise directly from the radicle or as branches of the primary root are spoken of as **adventitious.** The roots which grow out from planted tubers, bulbs, and rhizomes, or from stem cuttings of such plants as blackberry, geranium, and rose, are adventitious roots.

Classification of Root Systems.—In corn, wheat, and other grasses, in palms, and in many other kinds of plants, the primary root does not become the principal root but stops growing while the plant is still young. In such cases the functions of anchorage and absorption are taken over by numerous adventitious roots which grow out at the base of the stem. There results what is spoken of as a **fibrous root system.**

A root system which consists principally of an actively growing primary root with its branches (secondary roots) is called a **tap-root system** or **primary-root system.** The outstanding examples of this category are found in the carrot, beet, radish, turnip, and other plants in which the primary root is greatly enlarged for food storage. In most cases, as in the mallow and oak, the primary or tap root is not so conspicuously enlarged.

The Form of the Root System.—Just as we recognize great differences in the form of the shoot systems of our common plants, so we find conspicuous differences in the form of root systems. (Figures 59 and 60 illustrate various types of root systems.) Those of cereals and most grasses are shallow and in general assume

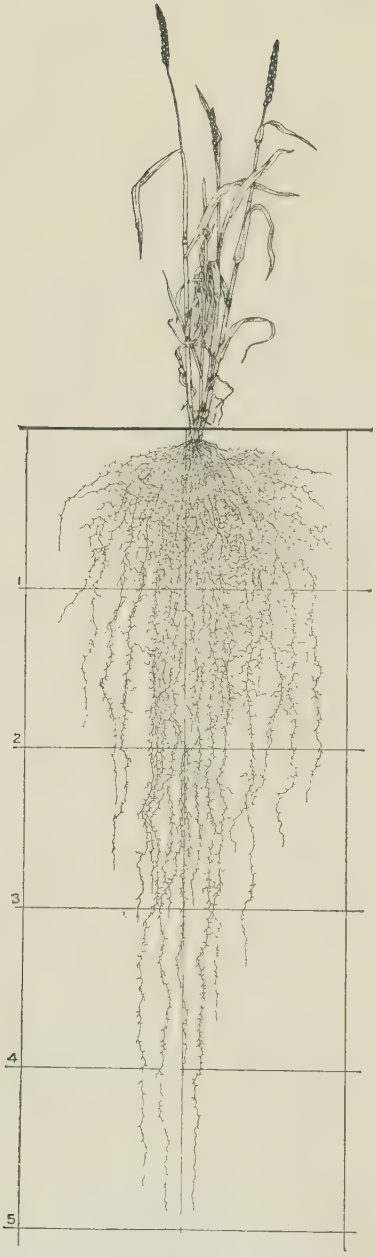


FIG. 59. Fibrous root system of wheat. The numbers indicate depth in feet. (After Weaver, Carnegie Institution of Washington, Pub. No. 316.)

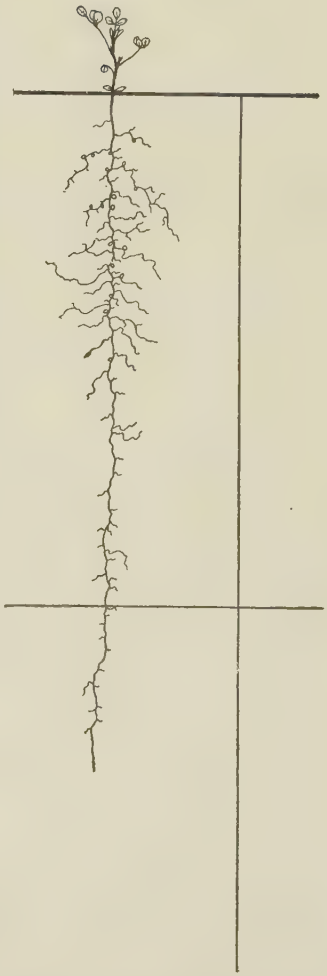


FIG. 60. Tap root system of young sweet clover plant (*Melilotus*). (After Weaver, Carnegie Institution of Washington, Pub. No. 316.)

a broad, pyramidal form, with the apex of the pyramid at the ground line. The sugar beet (*Beta vulgaris*), on the other hand, has a deep root system, the general form of which is rectangular.

Though shallow root systems are characteristic of certain species of plants and deep root systems of others, in many cases the depth of the root system varies greatly with soil conditions. Plants living in a dry region, where they must depend largely on occasional showers for water, profit by a shallow root system with great numbers of roots in the first few inches of soil, for beyond this the water seldom penetrates. On the other hand, for plants growing in regions where they must depend principally on water deeper in the soil, the deep root system is more advantageous. As far as firm anchorage of the plant is concerned, the deep root system is obviously more efficient than the shallow.

STRUCTURE OF ROOTS

External Features.—It will be recalled that a stem is divided into sections, and that at more or less regular intervals there are enlarged joints (nodes) from which leaves and buds arise, the portions between the nodes being called internodes.

Each individual root tapers very gradually, from its point of attachment to the stem or a larger root, towards its free end or **root tip.** By root tip is meant the 4 to 6 centimeters at the free end where growth in length, absorption of water and mineral salts, and most of the primary development of the tissues take place. This part of the root may be divided into the following regions, beginning at the extreme end:

The root cap.
The growing point or region of active cell division.
The region of elongation.
The region of root hairs.

The **root cap** is a special protective mass of cells covering the tender cells which constitute the growing point of the root. As a protective structure it corresponds to the rudimentary leaves and bud scales of the stem, though of entirely different structure. But whereas the latter protect mostly from injury due to water loss, the

root cap is concerned chiefly with protection against mechanical injury. As the root tip is constantly forced through the soil, the root cap bears the brunt of the abrasion and the outermost cells next to the soil are rubbed off against the soil particles as the root advances through the soil. To compensate for this wearing away, cells are constantly being added to the root cap by the meristematic cells (promeristem) of the growing point.

The growing point, as in the stem, consists of tissue (promeristem) in which active cell division continues as long as the root grows. In most cases this region of the root is about a millimeter long. Growth in length takes place in this region but at a very much slower rate than in the region of elongation just behind it. As the result of active cell division, the number of cells in the growing point tends to increase. Some of these cells are added to the root cap. Others are constantly passing over into the region of elongation.

In the region of elongation the cells have ceased dividing and are undergoing very rapid growth in length as the result of the absorption of large quantities of water and the stretching due to the high turgor thus developed. This region of the root is generally but 2 to 5 millimeters long. Thus only a minute section—a few millimeters—of the tip of the root is actually being pushed ahead through the soil.

In the region of root hairs, elongation has ceased and the surface of the root becomes clothed with a dense outgrowth of hairs. This region might also be called the zone of maturation, for in this region there is taking place within the root the differentiation of cells into vessels, tracheids, sieve tubes, and the various other permanent tissues of the root.

The four regions which have been briefly described are spoken of collectively as the root tip. In the part of the root behind the tip the root hairs are withered and dead, for the life of each root hair is but a few days, and the older ones die off as new ones are produced at the lower end of the root-hair zone. In the mature part of the root, growth in length never takes place; instead there sometimes is an actual shortening due to the contraction of tissues. It is in this region that secondary roots make their appearance.

Anatomy of the Root.—Since roots are much more uniform in their internal structure than are stems, we shall not have to study

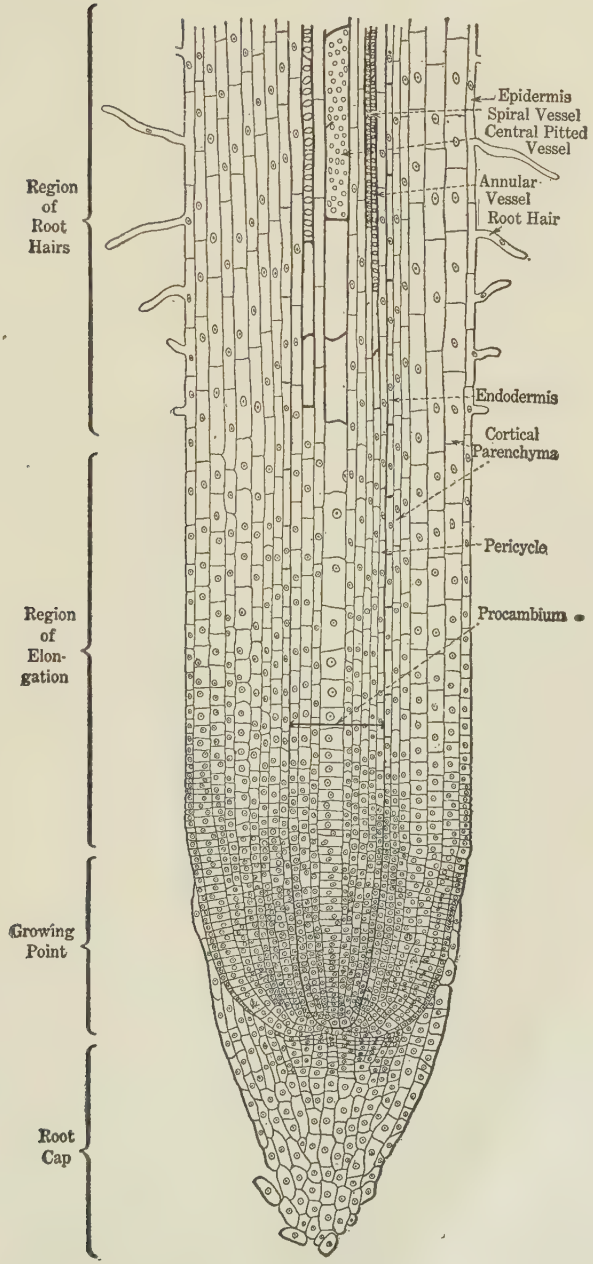


FIG. 61. Longitudinal section of the tip of the root of barley (*Hordeum sativum*).

several types, but merely consider a series of cross sections from the growing point to the mature region.

The Growing Point.—This is composed of typical meristematic cells, thin-walled, all very much alike, practically without intercellular spaces. During that time of the day when cell division is most active a great many nuclei are in some stage of mitosis.

The Region of Elongation.—Though most of the cells in this region are still meristematic, they no longer are uniform, for some

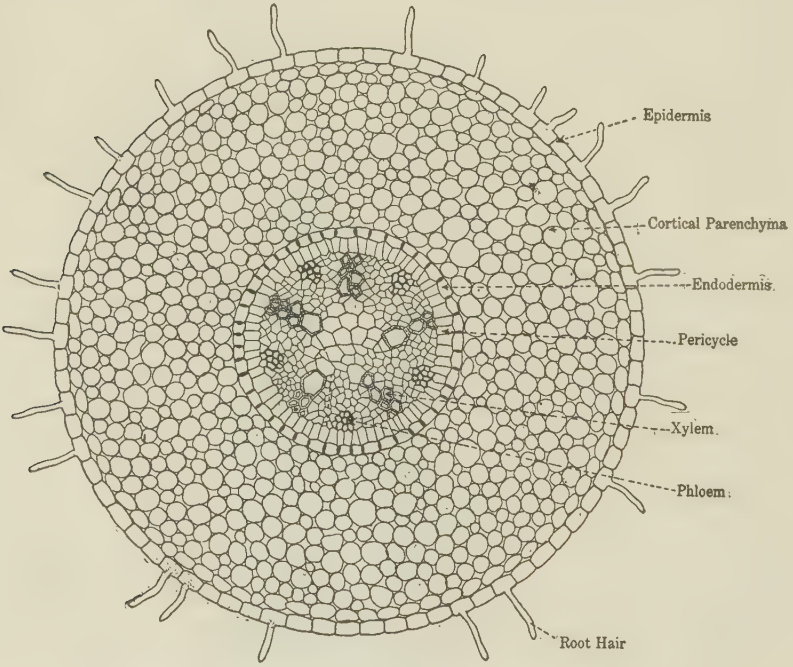


FIG. 62. Cross section (diagrammatic) through the root-hair zone of a young root.

differentiation has taken place. The single layer of surface cells constitutes the **protoderm.** The cylindrical group of cells in the center of the section is now the **procambium,** and between this and the protoderm is the **ground meristem.** It will be recalled from the discussion of the anatomy of the stem that these three meristematic regions are spoken of as the primary meristems.

The Region of Root Hairs.—In this region the following permanent tissues are present:

1. The **epidermis** (derived from the protoderm) with its root hairs.
2. The **cortex** (derived from the ground meristem), the innermost layer of which is the endodermis.
3. The **stele**, consisting of:

   The **pericycle**, which is derived from the ground meristem, and the **xylem** and **phloem** derived from the procambium.

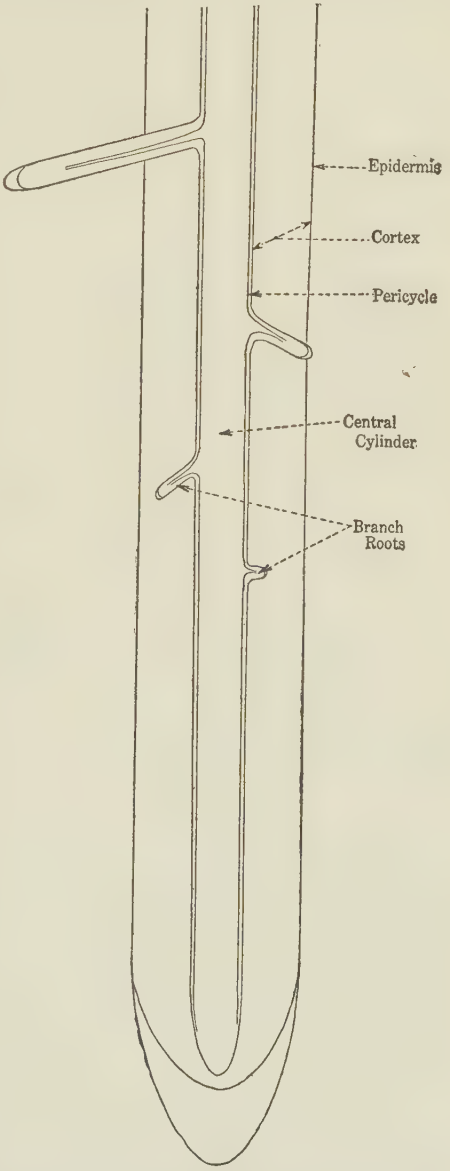


FIG. 63. Diagram showing the origin of branch roots and their emergence from the main root.

The epidermis consists of a single layer of cells from which the root hairs arise. The cortex is composed of numerous layers of parenchyma cells and of a single innermost layer, the endodermis. The cells of the latter frequently have their inner and radial walls thickened and impregnated with cutin and suberin.

The arrangement of the vascular tissues is of the radial type. The xylem elements are in groups which radiate from the center of the root. Alternate with, and in the angles formed by, these radiating xylem groups, are groups of phloem elements.

Root Branching.—It will be recalled that the outermost tissue of the stele is the pericycle. It is in this layer that branch roots have their origin. The first evidence of the formation of a branch root is the tangential division of certain pericycle cells. These form a group of meristematic cells, which in turn develop a root tip with root cap. The root tip makes its way outward through the cortex and the epidermis, and reaches the surface. Such branch roots do not emerge into the soil until elongation has ceased in that part of the main root from which they arise. It appears that root branching is encouraged in soils well supplied with nutrient salts, and retarded in soils deficient in these salts.

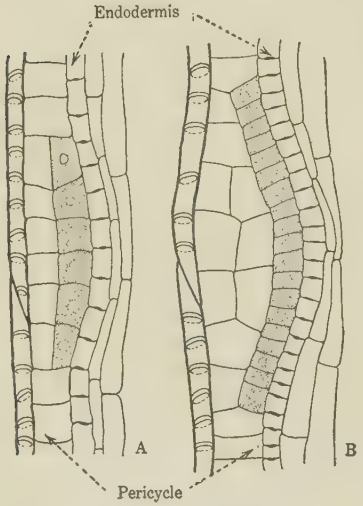


FIG. 64. Two stages in the development of a branch root. Certain pericyclic cells (here stippled) become meristematic, first undergo tangential division, and thus initiate the process of branch root formation. (Redrawn from Van Tieghem.)

Root Hairs.—We speak of the roots as the absorbing organs of the plant. In a sense this is true, but it must be understood that water and solutes are not taken in at all points on the surface of the root system. Practically all substances absorbed from the soil enter the plant through the epidermal cells which bear root hairs. This is well shown when plants are transplanted or disturbed in such a way as to destroy root hairs. We may see no apparent injury to the roots, but closer examination shows that many of the root hairs have been destroyed. Excessive watering will not make up for the loss of root hairs by transplanting. The roots may be surrounded by nearly saturated soil, but in the absence of root hairs they cannot absorb adequate amounts of water. Root hairs greatly increase the absorbing surface of a plant. For example, it has been computed that a corn plant with root hairs has an absorbing surface about six times that of one from which the root hairs have been removed. A root hair is a lateral outgrowth of an epidermal cell. A hair and the epidermal cell from which it grows are not separated by a wall but together

they constitute a single branched cell with a single protoplast. Though tending toward cylindrical form, root hairs may become greatly contorted in their growth between and around soil particles. They vary in length from a fraction of a millimeter to 7 or 8 millimeters, and have delicate walls composed of cellulose and pectic compounds. These are lined only by a thin layer of cytoplasm, and so the vacuole or vacuoles are relatively large. All the materials that enter the plant from the soil must pass through the walls and the cytoplasmic membranes of the root hairs or epidermal cells. From the root hair, the absorbed materials are passed on to cells of the root cortex, to the pericycle, and then into the conducting elements of the xylem. By these they are carried to various parts of the plant.

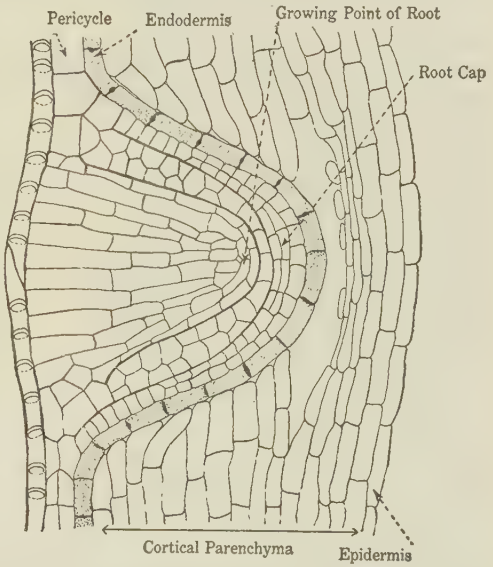


FIG. 65. Later stage than shown in Fig. 64, showing the development of a branch root. (Redrawn from Van Tieghem.)

Functioning root hairs are not found along the full length of the root, but appear as a white, fuzzy coating on a definite zone, known as the root-hair zone. If we proceed backward from the growing point we will find that this zone lies immediately beyond the region of elongation. Root cap, growing point, and region of elongation all are devoid of root hairs. Root hairs are short-lived, usually functioning for only a few days or weeks. New hairs are constantly formed at the lower end of the root-hair zone, while the old hairs at the upper end are dying. The root-hair zone advances through the soil as the root grows. In this way the hairs are constantly brought into contact with new soil particles as new soil regions are invaded. This is of advantage to the plant, first because new stores of water and salts thus become available to the root hairs,

FIG. 66. Seedling of garden cress (*Lepidium*) grown in moist air. Root hairs in various stages of development can be distinguished behind the region of elongation. Surrounding the cotyledons is the swollen gelatinous mass derived from the seed coats. Magnification 6×.

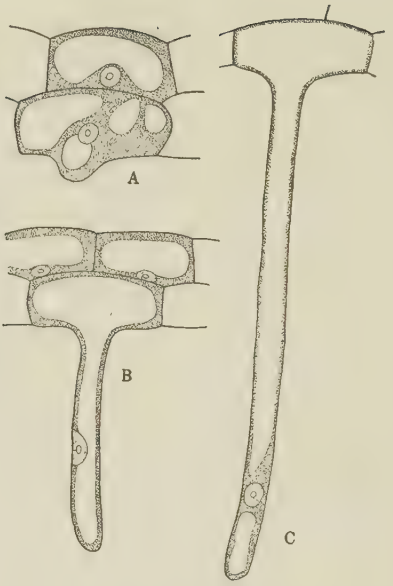


FIG. 67. Stages in the development of of a root hair. (After Frank.)

FIG. 68. The tip of a root hair showing adherent soil particles. Such particles, between and around which the root hair has grown, often become so firmly attached to the root hair that they can not be washed off or removed in any other way without injury to the root hair. (After Noll.)

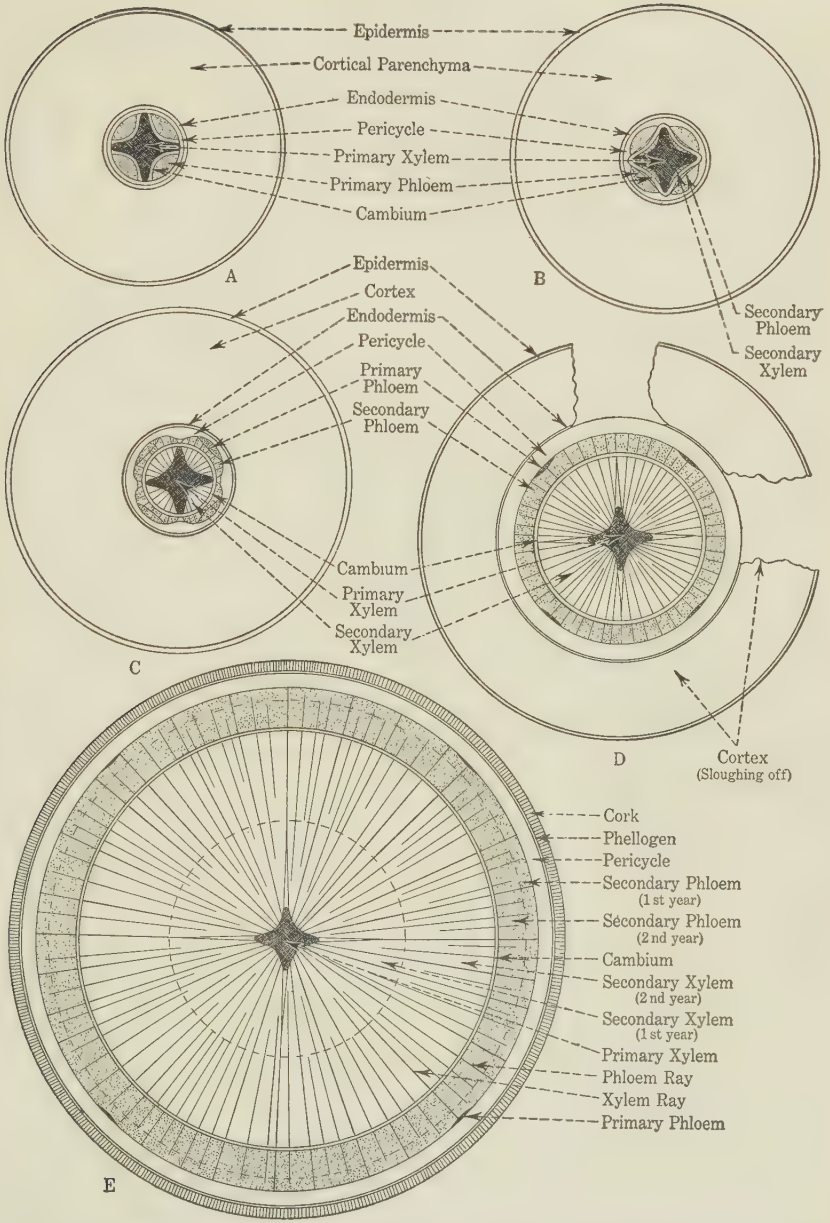


FIG. 69. Diagrams showing stages in the secondary growth in thickness of a root. *A*, before the appearance of cambium. *B*, the formation of the cambium ring. *C*, *D*, and *E* stages in the development and growth of secondary phloem and xylem. Secondary increase in thickness due to the activity of phellogen is also shown. (Drawing prepared by Esau.)

and, second, because these new soil regions are devoid of any deleterious substances which may accumulate in the neighborhood of the old hairs.

The root hairs of some plants persist for many months. For example, those of honey locust (*Gleditsia triacanthos*) become thick-walled and brownish in color and may live for several months; and those of certain species of the composite family may persist for several years.

Growth in Diameter of Root.—In most monocotyledons and in many annual dicotyledons there is no secondary increase in thickness in the roots. That is, there is no formation of rings of growth in such roots as in woody stems. This means that in such plants, sections through older parts of the root, and many inches back of the root tip, would be essentially like a section through the region immediately behind the root-hair zone. In these older parts of the root, the root hairs are withered and dead, and the epidermal cells and frequently several adjacent layers of cortex cells become suberized and function as a protective layer.

Fig. 70. Diagram showing a root hair, *h*, which is an outgrowth of the epidermal cell, *e*, and which has grown between the soil particles. α, β water surface, δ air spaces. Water indicated by parallel curved lines, soil particles by shading with straight lines. (After Sachs.)

In perennial dicotyledon and gymnosperm roots, however, there is secondary increase in thickness. This generally progresses in the following manner: First, certain of the parenchyma cells adjacent to the outside of the xylem strands, and to the inside of the phloem strands, including cells of the pericycle lying just outside of the xylem masses, become meristematic and form a cambium ring. As a result of the activity of this cambium ring, new xylem groups are formed inside the cambium across from the original phloem strands, and thus vascular bundles similar to those of dicotyledonous and gymnosperm stems are produced which grow by the production of additional phloem on the outside and xylem on the inside.

Soon after the vascular cambium makes its appearance, certain cells of the pericycle become meristematic and form a **phellogen** or **cork cambium**. The cork cambium produces cork externally and phelloderm internally. All the tissues which originally lay outside the pericycle die soon after cork formation commences. As a result

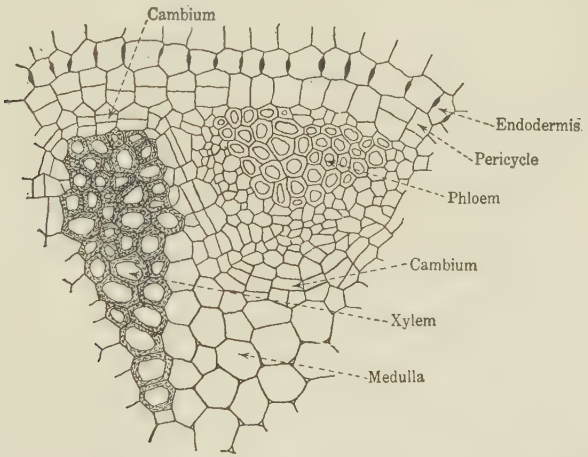


FIG. 71. Cross section of a portion of the central cylinder of a primary root of horse-bean (*Vicia faba*), showing the origin of the cambium. (Redrawn from Haberlandt.)

of the activities of the two cambiums, the old root comes to resemble closely an old stem in structure.

FUNCTIONS OF ROOTS

The functions of the root system are **absorption, conduction, anchorage,** and **storage.** These four processes will be described in the order named.

In considering the process of absorption we shall discuss: (*a*) absorption of water; (*b*) absorption of inorganic salts.

Absorption of Water.—Water performs many essential rôles in the plant, chief of which are the following:

1. It is a necessary component of protoplasm, constituting about 80 to 90 per cent of the weight of active protoplasm.

2. It is an essential raw material for food manufacture (see page 131).

3. It serves as a solvent of gases (oxygen and carbon dioxide).

4. It serves as a medium of transportation of raw materials and foods from place to place in the plant, since their transport can occur for the most part only in solution.

5. It makes possible the maintenance of turgor in living cells, and the plant functions normally only when the cells are distended with water.

Water is the chief limiting factor in the growth of most crops. For the majority of crops, there is ample sunshine and an abundance of oxygen and carbon dioxide in the air; the temperature of the air and soil is seldom seriously unfavorable; and, as a rule, there is sufficient of the necessary mineral substances in the soil; but except in the agricultural regions where the rainfall is unusually great there is generally at some time during the season a shortage of water. This is particularly true in arid and semi-arid regions.

Water is a most important factor in determining the distribution of plants over the earth's surface. The striking differences in the vegetation of the high mountains, the dry plains, and the prairies, in that of the tropical rain forests, deserts, and tundra, and in that of hillside, brook-bank, gravel slope, bog, meadow, and open water are largely due to differences in the available water supply.

The entrance of water into the plant which takes place through the root hairs is spoken of as **water absorption.** Water passes out of the plant principally through small openings (stomata) in the surface of the leaves, and we speak of this water exit as **transpiration.** From roots to leaves there is a continuous stream of water through the plant. It is at two points, the point of entry and the point of exit, that its rate of flow is most likely to be restricted. Too much transpiration and too little absorption are the principal dangers to which the plant is exposed.

All substances, whether themselves gases or solids, which enter the plant from the soil must be in solution in water, and must pass through the wall of the root hair and also through the cytoplasmic membrane which lines the wall. The cell wall, which is of cellulose, is a permeable membrane. Water and all solutes present in the soil solution can pass through this wall unhindered. The cytoplasmic membrane, however, is semipermeable. Normally, the total concentration of the solutes (number of dissolved particles in a given

volume) in the cell sap of the root hair is greater than in the soil solution outside the root hair. Under this condition the movement of water is from the soil into the root hair, and this movement of water tends to go on just as long as the concentration within the root hair exceeds that outside. Water, however, is constantly being withdrawn from root-hair cells to the outermost cells of the cortex. This causes the concentration of the cell sap of the root hairs to remain fairly constant. The water passes across the endodermis and pericycle to the xylem of the root, by which it is carried upward into the stem and thence to the leaves.

Water in the Soil.—Soil is a granular material consisting largely of minute particles of rock of irregular shape together with fragments of organic material of plant or animal origin. On account of the varying size and irregular form of the soil particles there are many spaces between the particles. The size of these spaces or pores varies greatly. If the soil is very dry most of the pores are almost completely filled with air, but when there is a heavy rain the air is forced out of all the spaces, large and small, between the soil particles and they become filled with water. After the rain stops part of the water in the pores is soon carried downward by gravity and is replaced by air. (This is of advantage to plants, for most plants cannot secure enough oxygen for the respiration of their roots and accordingly soon die if all the pores of the soil are filled with water.) A considerable amount of water is still held by capillarity in the pores. It is this condition of the soil when the pores are partly filled with air which is favorable for the growth of most plants.

When roots continue to absorb water from the soil the moisture content may be reduced to a degree at which it is difficult for the plant to secure more water and, if no more water is added to the soil, the roots are finally unable to overcome the force of capillarity.

Before this point is reached the quantity of water being absorbed may have become less than that which the plant is losing by transpiration, and the plant shows evidence of wilting. The condition of such a plant is called **temporary wilting**, for absorption has not ceased entirely and the plant may recover its turgor if transpiration is reduced as it is at night when the air becomes cooler and more humid.

As transpiration continues a stage of wilting is reached at which the plant will not recover, even though placed in a saturated atmosphere, unless water is added to the soil. The plant is now in a condition of permanent wilting.

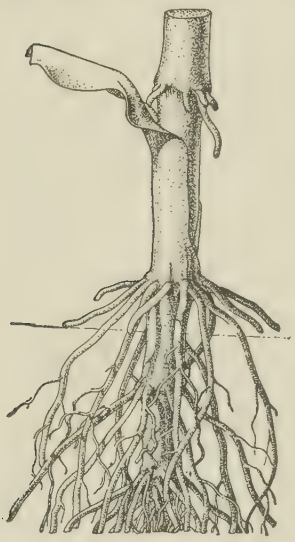


Fig. 72. The aerial or "prop" roots of corn (*Zea mays*).

Thus temporary wilting is a condition from which the plant may recover if transpiration is greatly reduced whereas recovery from permanent wilting is possible only if more water is added to the soil.

A wide range of moisture content of the soil appears to be equally favorable to the growth of plants. As long as the soil is not saturated and is not so dry that it is approaching the condition which would produce permanent wilting, the moisture conditions are suitable for active growth. In other words, within this range there seems to be no optimum moisture content.

Absorption of Inorganic Salts.—Land plants derive their inorganic salts from the soil. Among the inorganic salts which occur in the soil, the chief ones used by green plants are nitrates, phosphates, and sulphates. Green plants derive nitrogen principally from nitrates; phosphorus from phosphates; and sulphur from sulphates; and the essential metallic elements, potassium, calcium, magnesium, and iron, are derived chiefly from nitrates, sulphates, and phosphates of these metallic elements in the soil. These salts can enter the plant from the soil only when they are in solution. The cytoplasmic membranes are permeable to them.

It is important to keep in mind, however, that under similar conditions the different inorganic salts move into the plant independent of the passage of each other and of water. A plant that absorbs twice as much water as another plant does not necessarily absorb twice as great a quantity of inorganic salts or of any particular salt. For the conditions governing the entrance of any particular solute into the plant, see the discussion on page 39.

We may picture the process of absorption by root hairs as one in

which the molecules of water and the dissolved particles of many different salts are independently diffusing through cytoplasmic membranes of the root hair at varying rates.

Whereas many soluble substances may pass from the soil through the cytoplasmic membrane into the root, it should be pointed out that water and carbon dioxide are the only substances in the cell sap of the root hairs which pass into the soil in large amounts. The supposition that under certain circumstances sugar in the beet root, for example, passes from the root into the soil is not correct. The percentage of sugar in the root may fluctuate as a result of changes in the quantity of water present, but normally the total quantity of sugar in the root does not decrease appreciably except when it is drawn upon for the growth of the shoot, or used up in respiration.

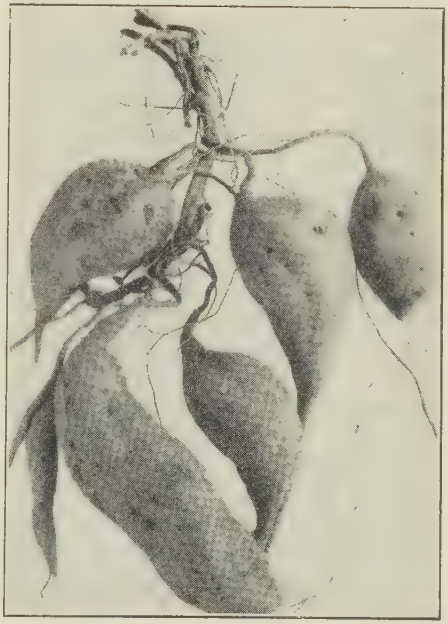


Fig. 73. Large quantities of food are stored in the roots of the sweet potato (*Ipomoea batatas.*)

On the other hand, movement of carbon dioxide (produced by respiration) from the roots into the soil can easily be demonstrated. It unites chemically with water to form carbonic acid (H_2CO_3), which aids in dissolving certain mineral inorganic compounds difficultly soluble in water.

Conduction by Roots.—Water which is absorbed by the root hairs passes into adjoining cortex cells and then across the root from one cell to another to the vessels and tracheids of the xylem. It is carried upward in these tissue elements to the stem. In the young root, xylem and phloem elements occur in radiating groups, the groups of xylem elements alternating with the phloem groups. This arrangement of the tissues is apparently of advantage because it makes it possible for the water to reach the xylem elements from

the cortex without first passing across the phloem elements. The dissolved mineral salts which are absorbed by the root hairs probably travel upward with the water in the xylem of the root and stem.

Anchorage.—The roots of a plant are very effective anchorage organs. In most plants all roots perform the triple rôle of absorption, conduction, and anchorage. However, there are some plants (cacti, e.g.) which are equipped with two kinds of roots, those mainly for anchorage and those chiefly concerned with absorption. The anchorage roots of the cactus are strong and descending, whereas its absorptive roots are weak and horizontal. The hold which roots have on the soil is well shown in plants of sand dunes; here, where the sand tends constantly to shift, mounds of sand are held in place by the mat of roots.

Our attention has been directed the last few years to the rapidly accumulating ill effects of soil erosion of agricultural lands. It is estimated that of the total land area of the United States, excluding badlands, mesas, and mountains, about 282 million acres have been seriously damaged or wholly ruined by soil erosion. In addition, approximately 775 million acres have lost one-fourth to three-fourths of their topsoil. In the cotton, corn, and tobacco belts, erosion by water is most acute, whereas in the Great Plains wind is the principal cause of erosion. Various methods are employed to control soil erosion, one of the chief ones being the growing of plants with root systems which will bind the soil and prevent it from washing or blowing. The living network of roots of perennial grasses is particularly effective in anchoring soil and preventing its erosion. The efficiency of roots as soil-binders is realized when we consider the enormous area of possible contact. Recently a worker made a quantitative study of the number, length, and total exposed surface area of the roots and root hairs of one rye plant. This plant had 13,815,762 roots and over 14 billion root hairs, the combined surface area of which was 6875.4 square feet. In this one rye plant the combined length of all its roots was 387 miles.

Storage.—The roots of many plants store food and water. Such roots may become large and fleshy, familiar examples being the sugar beet, turnip, carrot, and sweet potato. Many plants with fleshy roots are cultivated for their roots alone and are called "root crops." Sugar and starch are the principal forms of food stored in such roots. The roots of perennial plants store large quantities of foods, even though they are not greatly enlarged and fleshy. For example, in the fruit trees both large and small roots are very rich in stored food. The roots of alfalfa and red clover are filled with starch. In

asparagus there are great masses of rather fleshy roots which serve as storage organs. In this plant the young edible shoots which grow up in the spring are made wholly at the expense of food stored in the roots. The persistence of some weeds, such as the dandelion, is due to the large amounts of food stored in the roots, and also to the ability of the roots to produce new leafy shoots when cut into pieces.

Reproduction by Means of Roots.—Some plants send up stems (so-called "suckers") from adventitious buds which arise on roots. This habit is well illustrated by the silver-leaf poplar (*Populus alba*) and the black locust. (*Robinia pseudacacia*). Plants which normally do not produce such adventitious buds may be induced to do so by injury. Similar reproduction from roots occurs in the red raspberry, some roses, and the common barberry (*Berberis vulgaris*). If the shoots of any of these are entirely cut off, the roots send forth new stems. Generally those plants which have a tendency to produce suckers from the roots can be propagated readily by means of root cuttings.

CHAPTER VI

THE LEAF

The principal part played by the green plant in this world of ours is to absorb and store a part of the tremendous quantity of energy which that great star, the sun, is continuously sending across the millions of miles of space which lie between it and our planet. All the energy utilized in the life processes of plants and animals, as well as in industry and transportation, is but the energy of sunlight transformed into heat, mechanical energy, electricity, chemical energy, and other forms of energy.

Sunlight is the sole source of the energy without which no single living thing, whether plant or animal, could continue to exist.

The life activities of plants and animals can go on only if energy is constantly supplied to them. All this enormous quantity of energy necessary for living plants and animals on the earth is absorbed, or, as we might say, "caught and held," by the green leaves and other green parts of plants. A small part of the energy used in the transportation and industry so characteristic of our civilization comes from falling water, raised, by direct action of sunlight, to the hills and mountains, whence it may flow downward through the turbines of hydro-electric stations and supply energy for conversion into electricity. But by far the greater part of the energy used in transportation and industry was also absorbed by green plants from sunlight and stored in wood, coal, or petroleum, which directly or indirectly are plant products.

Thus the green plant is the great "converter of solar energy"; it transforms the energy of sunlight into other forms utilizable by plants and animals and by all the machines and devices of modern civilization which furnish us with light, heat, transportation, and other useful applications of energy. This process of energy transformation by green plants is called **photosynthesis** (Greek, *photos*, light, and *synthesis*, putting together) because it involves the union

of carbon dioxide and water to form sugar. One of the striking characteristics of a green plant is the continuous accumulation within it of organic compounds (sugars, fats, proteins, etc.). These are not absorbed from outside the plant, but are built up within the plant out of simple inorganic compounds, such as water, carbon dioxide, and various mineral salts.

The dominant color of the world is green. This color is due to a pigment known as **chlorophyll**. We know that chlorophyll plays an indispensable rôle in the conversion of solar energy to the potential energy of organic compounds. Although young stems are green in color, the leaves make up by far the greatest part of the chloro-

FIG. 74. Simple leaf of pear, showing stipules.

phyll-bearing tissue of the plant. Thus, the green leaf is the principal agency in the utilization of light energy from the inexhaustible supply furnished by the sun, and in the conversion of it into the energy stored in food, which is used by plants and animals alike. The food serves not only as a means of storing energy which the plant or animal can later use for its life processes but also as material for the construction of new protoplasm and cell walls. Photosynthesis is the primary function of the leaf. It is the leaf also, from which most of the water of the plant passes off into the atmosphere—a process known as transpiration.

We take leaves for granted; they are so commonplace that we overlook their great importance. Not only in the particulars mentioned above are they important, but much of the beauty of the landscape is due to their color and form. Many ornamental plants owe their attractiveness quite as much to their foliage as to their flowers. Leaves are also used directly as food by man and other

animals; in fact, they are the chief food of all herbivorous animals, and man himself utilizes commercially the leaves of a variety of plants, such as lettuce, endive, spinach, celery, parsley, cabbage, tea, and tobacco.

Principal Parts of a Leaf.—The leaf is one of the most distinctive of plant structures. Its outward form and internal structure make it well adapted to perform the functions of photosynthesis and transpiration. The most conspicuous and important part of an ordinary leaf is the broad, thin **blade**, consisting for the most part of the veins, and the soft, green tissue, known as **mesophyll** (Greek: *meso*, middle, and *phyll*, leaf), supported by the veins. Most leaves have a **stalk** or **petiole** which attaches the blade to the stem and through which materials are conducted to and from the leaf. Some leaves, such as those of grasses, have no petioles, and are said to be **sessile** (meaning, sitting). Frequently there are outgrowths, often leaflike, from either side of the leaf base. These two small appendages are called **stipules**. Stipules are characteristic of the leaves of certain families of plants, such as the bean family, whereas in other plant families, for example the mustard family, the leaves bear no stipules.

FIG. 75. A portion of a stem of pimpernel (*Anagallis*), showing the sessile leaves.

Venation.—The most casual observer has noticed the great difference in the arrangement of the veins in leaves of different kinds of plants. For example, in grasses, lilies, and related plants (together forming a very large assemblage of flowering plants known as the monocotyledons), the veins that are clearly visible to the unaided eye run parallel to each other either the full length of the blade or from the stout midrib to the margin of the leaf. This type of venation is known as **parallel venation**. If such a leaf is examined with a lens, it can be seen that small

veinlets connect the more distinct parallel veins. In most of our broad-leaved plants, such as the oaks, apple, cotton and grape, which together form a large group of plants known as the dicotyledons, the veins that are visible to the naked eye branch frequently and join

FIG. 76. Compound leaf of garden pea (*Pisum sativum*). Note the large, leaf-like stipules and upper leaflets, modified as tendrils. (From Bocquillon.)

again, so that they form a network. This type of arrangement of the veins is known as **net venation**. In the net-veined leaves, there may be a single principal vein or midrib from which the smaller veins extend, somewhat as do divisions of a feather. Such leaves are **pinnately veined**. Familiar examples are the willow, cherry,

and apple. In other plants, such as the maple, melon, and grape, there may be several principal veins spreading out from the upper end of the petiole. Such a leaf is palmately veined.

Fig. 77. A branch of European linden, *Tilia europaea*, its leaves forming a mosaic.

Form of the Leaf Blade.—We have come to recognize a great many plants by the form or outline of the leaf blade alone. Certain leaf forms are typical of whole groups of plants. The commonest form of leaf is one in which the blade is all in one piece, as in the violet, maple, apple, etc. Such a leaf is said to be simple. The

blade of simple leaves frequently has a number of lobes separated by clefts. Familiar examples of such **lobed** leaves are those of the oak and maple. Another familiar form of leaf is one in which the leaf

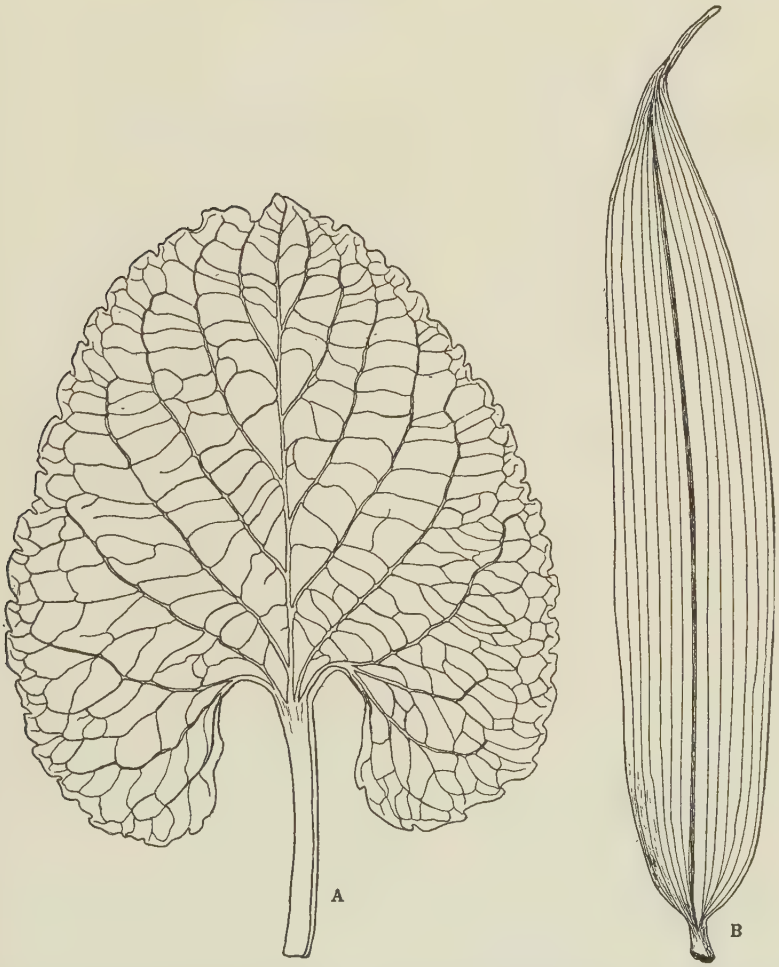


FIG. 78. The two principal types of venation. *A*, Net venation as illustrated by the leaf of violet (*Viola*); *B*, parallel venation illustrated by the leaf of one of the bamboos. (*Arundinaria.*)

blade consists of a number of separate leaf-like parts, called **leaflets.** Such a leaf is said to be **compound.** Examples of compound leaves are the leaves of clover, most ferns, the carrot, and the rose.

There are many different kinds of simple and compound leaves. They vary in size, in shape, in character of margin, in nature of lobing, in number of leaflets, and in various other characters.

FIG. 79. *A*, The simple, pinnately veined leaf of a plum (*Prunus*); *B*, the pinnately lobed, and pinnately veined leaf of an oak (*Quercus*); *C*, the palmately lobed and palmately veined leaf of a maple (*Acer*); *D*, the palmately compound leaf of wood-sorrel (*Oxalis*); *E*, the pinnately compound leaf of walnut (*Juglans*).

Anatomy of the Leaf.—As we have already said, the primary functions of the leaf are (1) manufacture of sugar from carbon dioxide and water (photosynthesis) and (2) transpiration. Let us now consider the leaf in relation to its structural adaptations to carry on these two activities. The absorption of the large quantities of carbon dioxide and light energy necessary for photosynthesis is favored by the very great surface exposed by the leaf blade. The thinness of leaves and the transparency of the colorless surface layer of cells (epidermis) facilitate the penetration of light to all the

green cells. Furthermore, through the epidermis there are many small openings called stomata (Greek, *stoma*, mouth; plural, *stomata*) through which gases, including chiefly carbon dioxide, oxygen, and water vapor, pass in and out of the leaf. The epidermis is usually coated with a thin waxy layer, the cuticle, which prevents excessive loss of water from the underlying tissues. The midrib and larger veins reinforce and give mechanical strength and relative rigidity to the thin sheet of cells which constitute the leaf blade. The elongated and rather thick-walled cells making up the midrib and veins are clearly well adapted to give support and also to conduct materials to and from the mesophyll leaves. In short, leaf anatomy is intimately related to leaf function.

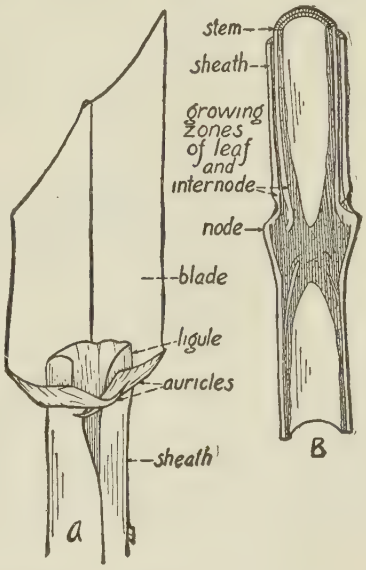


FIG. 80. *A*, Portion of leaf of barley at the juncture of sheath and blade; *B*, stem cut in median lengthwise section. ×2½. (After Robbins, from *Botany of Crop Plants*.)

Microscopic examination of a cross section of a typical foliage leaf shows three tissue regions: (1) the **epidermis**, (2) the **mesophyll**, and (3) the **veins** (vascular bundles). The epidermis consists of a thin, transparent layer, relatively impervious to water vapor, which covers the whole leaf surface and protects the tissue below it, not only from mechanical injury, but also from drying out. The mesophyll is made up of relatively large, thin-walled cells, most of which are green and able to carry on photosynthesis. The veins consist of conducting elements which serve to transfer water and inorganic salts and foods and, in the larger veins, of very thick-walled cells which give them considerable rigidity and mechanical strength.

The Epidermis.—The total area of the leaf constitutes a very large part of the whole plant surface which is exposed to the air. Because of this, the ability of the leaf epidermis to retard transpiration is of the utmost importance to the plant.

When a piece of epidermis from the lower side of a leaf is examined under the microscope it is found to consist of two kinds of cells, ordinary epidermal cells and guard cells. As seen in

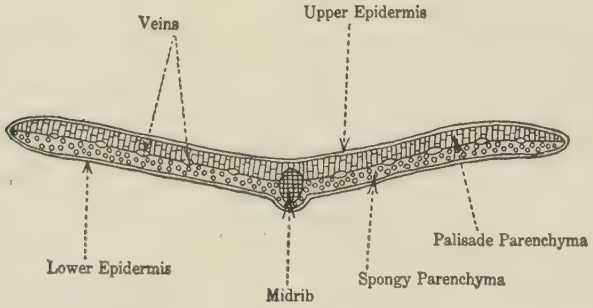


FIG. 81. Diagram of a cross section of a typical foliage leaf.

surface view, the ordinary epidermal cells of the leaves of most plants have a wavy outline (Figs. 82 and 83). In cross sections of leaves it can be seen that the depth (radial diameter) of the ordinary

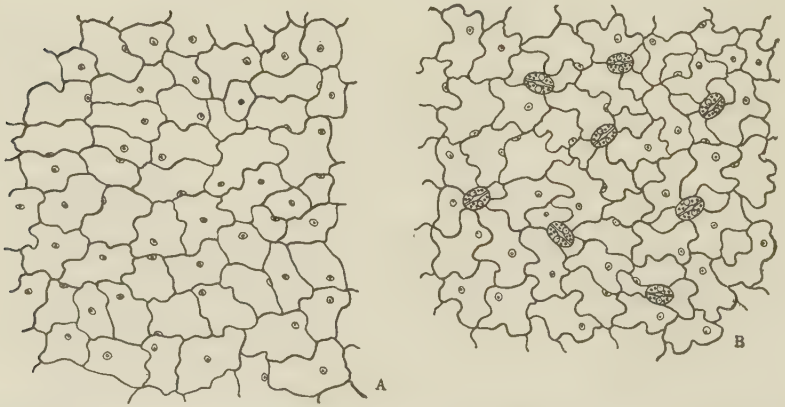


FIG. 82. Surface view of the epidermis of a leaf of *Senecio mikanoides*. *A*, from the upper surface of the leaf; *B*, from the lower surface. The cytoplasm of the cells has not been shown.

epidermal cells is considerably less than their breadth or length (Fig. 78). In most species of plants, chloroplasts are not found in the ordinary epidermal cells. The leaf epidermis, like that of the younger parts of the stem, has the outer walls of its cells provided

with a waterproof surface layer, the cuticle, consisting almost entirely of the waxy substance, cutin. Beneath this there may be a cellulose-cutin wall layer spoken of as the cutinized layer. The innermost layer of the outer wall and all of the other walls of the epidermal cells consist of almost pure cellulose.

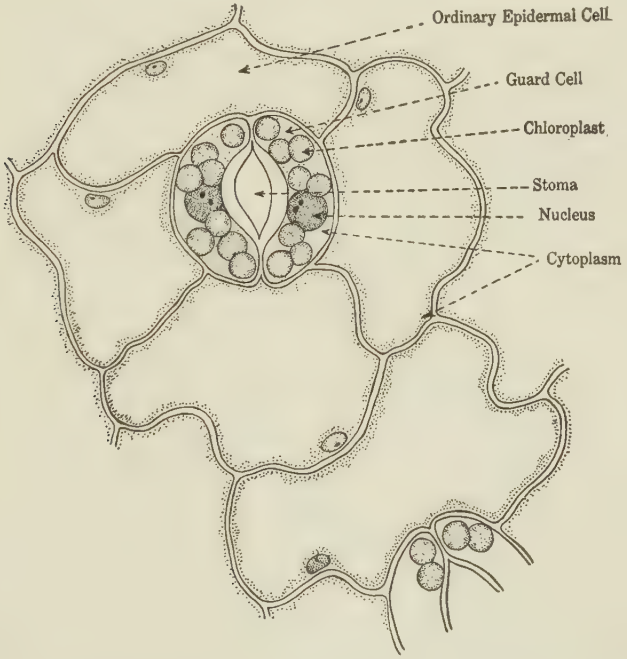


FIG. 83. A view showing in detail a small portion of the epidermis from the lower surface of a typical leaf.

In the chemical control of annual weeds, such as wild mustard, which may infest grain fields, advantage is taken of the difference in the nature of the leaf surfaces of various plants. For example, the epidermis of cereal leaves is covered with a waxy cuticle, whereas that of the wild mustard and certain other broad-leaved annuals is not so heavily cutinized. When a field of grain infested with such weeds is sprayed with a toxic chemical dissolved in water, the liquid runs freely off the cereal leaves but adheres to those of the rough-leaved weeds. The principal herbicides now employed to kill weeds in grain fields are dilute sulphuric acid, sodium dinitro-ortho-cresylate ("Sinox"), and iron sulphate.

The cytoplasm of the epidermal cells of the leaf forms a thin layer surrounding a large vacuole, and the nucleus and nucleolus

are often very conspicuous. The protoplasts of the epidermal cells are long-lived; they do not die until just before the leaf falls. In most plants, the ordinary epidermal cells are devoid of chloroplasts.

Guard Cells and Stomata.—Scattered among the ordinary epidermal cells of the lower epidermis, and sometimes of the upper epidermis also, are the guard cells, which occur in pairs. When seen in surface view they appear broadly crescent-shaped or almost semicircular in form (Fig. 83). In each pair of guard cells, the more or less concave sides of the cells are in contact, and between them there is an opening or pore which leads from outside the leaf into one of the large air chambers of the mesophyll. This opening between the guard cells is the stoma. Since the cuticle of the leaf

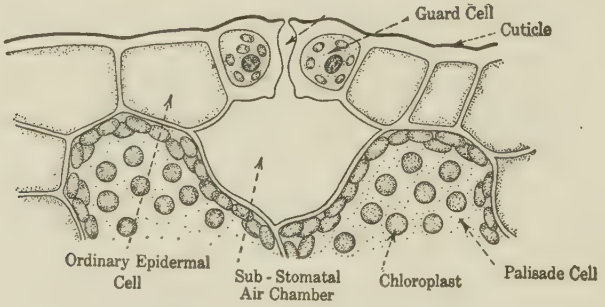


Fig. 84. A portion of a cross section of a foliage leaf showing a stoma and a few of the neighboring cells. (Redrawn after Kny.)

is generally quite impermeable to oxygen, carbon dioxide, and water vapor, the passage of these three gases, mostly by diffusion, into or out of the leaf takes place very largely through the stomata.

The guard cells, unlike the ordinary epidermal cells, contain numerous conspicuous chloroplasts. In cross sections of the leaves of many kinds of plants it can be seen that the walls of the guard cells on the side adjacent to the stoma are of greater average thickness than elsewhere. There may also be observed ridge-like outgrowths from the walls of the guard cells, which form a chamber, or vestibule, outside the stoma proper. Sometimes the vestibule has only a narrow, slit-like opening to the outside. In plants of dry habitats the ordinary epidermal cells may overlap the guard cells so that the stoma and guard cells are depressed below the general surface of the epidermis.

Control of the Stomata by the Guard Cells.—By changes in their turgor the guard cells are able to open and close the stomata, thereby regulating the entrance and exit of gases to and from the interior of the leaf. The stomata open when the turgor of the guard cells rises; increased turgor of the guard cells is due to an increase in the concentration of their cell sap which enables them to absorb water from neighboring cells; increased concentration of the cell sap is due to an increase in sugar in the guard cells. Since the stomata generally open when the leaf is illuminated it was formerly the belief that this increase in sugar in the guard cells was due to photosynthesis. It now appears that light in some way, not yet clearly understood, causes the starch grains in the guard cells to be (digested) transformed into sugar although in the mesophyll cells of the leaf, starch grains are formed in the light and disappear in the dark. The stomata close when the turgor of the guard cells falls; decreased turgor of guard cells is due to decrease in the concentration of their cell sap, which lowers their power to absorb water from adjacent cells; decreased concentration of the sap of the guard cells results chiefly from the sugar being transformed again into starch.

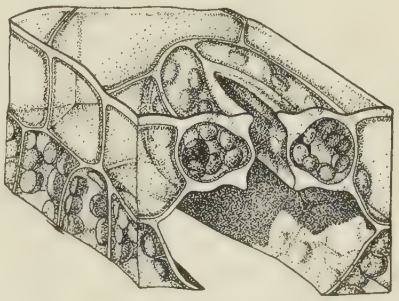


FIG. 85. Diagram showing a typical stoma and adjoining epidermal cells as seen in surface view and in cross section.

Epidermal Hairs.—Many leaves have hairs growing out from the epidermis. When epidermal hairs are present they are generally much more abundant on the lower than on the upper side of the leaf, and frequently are restricted to the former. The simplest of these hairs are mere extensions of epidermal cells, the hair and the epidermal cell together constituting but a single cell, as in the Cruciferae (mustard family). Multicellular epidermal hairs, consisting of a single filament of cells decreasing in diameter from the base to the apex, are much more common than are unicellular hairs. Many species of plants have branched hairs which may be either unicellular or multicellular. Glandular hairs which secrete ethereal oils and various other substances occur on the leaves of many plants.

The Mesophyll.—The two surfaces of typical foliage leaves are usually distinctly different in appearance. The upper surface is generally darker than the lower, and the larger veins project from the surface on the under side, but on the upper side are even with the leaf surface or depressed below it. The green tissue between the upper and the lower epidermis is called the mesophyll.

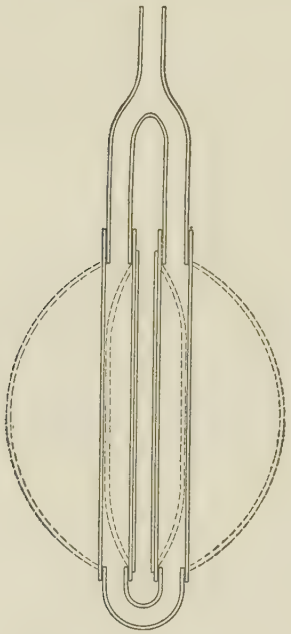


FIG. 86. Diagram of a model illustrating the manner in which one type of stomatal apparatus is opened when the turgor of the guard cells increases. The short glass U-tube shown at the top of the figure is connected to the Y-tube, also of glass, by two pieces of rubber tubing. The inner (adjacent) walls of these two pieces of tubing are made thicker than their outer walls. The thicker portions of the walls of the rubber tubing corresponds to the guard cell walls nearest to the stoma. If water or air is forced under pressure into the Y-tube and the rubber tubing thus subjected to internal pressure, the greater extensibility of the thin, outer walls causes them to take the position shown by the outer dotted lines in the diagram. As the result of this bulging of the outer walls of the rubber tubes the inner, thick walls are drawn apart as shown. Thus, under pressure from within the tubes, the space between the tubes is widened, corresponding to the opening of the stoma. When the pressure is reduced the inner walls tend to return to their original position, narrowing the opening between them, as when the stoma is closed by the guard cells.

The mesophyll is generally made up of two kinds of tissue: the **palisade parenchyma** and the **spongy parenchyma.** The palisade parenchyma consists of one to several layers of elongated green cells placed at right angles to the leaf surface. It extends downward from the upper epidermis to the spongy parenchyma. The palisade parenchyma is much more compact than the spongy parenchyma, a fact which is responsible for the darker color of the upper surface of most leaves. Intercellular spaces are by no means absent, however. These spaces are smaller than those of the spongy parenchyma but they are so distributed that every palisade cell is in contact with an intercellular space. Moreover, each

such space communicates with the system of connecting intercellular spaces in the spongy parenchyma so that if one were small enough it would be possible to enter a stoma, find one's way about in the intercellular spaces between the cells, and emerge through another stoma quite distant from the point of entrance. Thus there is provision for

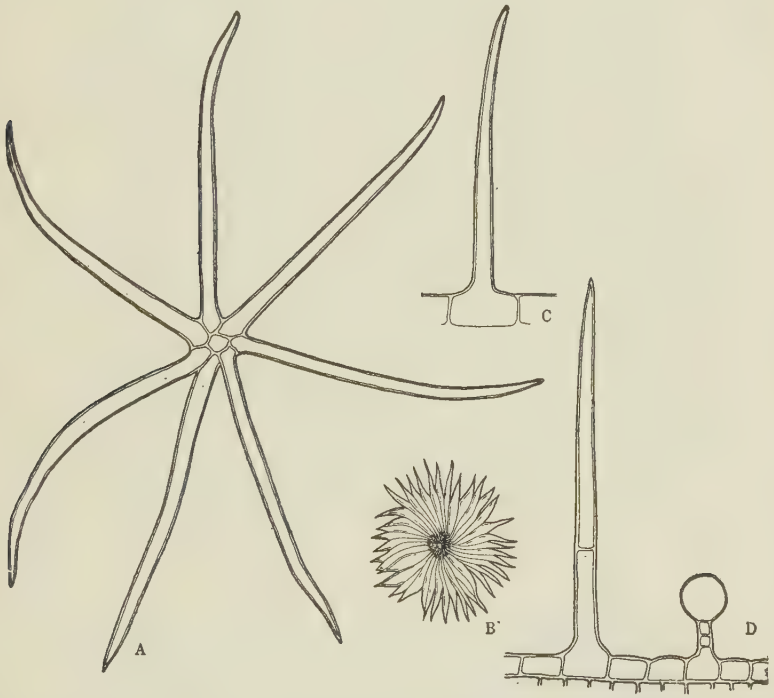


FIG. 87. Several types of epidermal hairs. *A*, branched hair of false mallow (*Malvastrum*), this hair is attached to the leaf by a short stalk not shown in the drawing. *B*, scale-like stellate hair of *Eleagnus*, its centrally attached stalk not shown. *C*, pointed, unicellular hair of shepherd's purse (*Capsella*). *D*, a pointed multicellular and a capitate, glandular hair of geranium (*Pelargonium*).

the free movement of carbon dioxide and oxygen to and from all the green food-making cells of the mesophyll. The palisade cells are more abundantly provided with chloroplasts than are the spongy parenchyma cells and because of their position receive more illumination than the spongy parenchyma cells.

The spongy parenchyma in typical leaves forms the lower portion (generally somewhat more than half) of the mesophyll. The cells

are not elongated like the palisade cells, and their form and arrangement are such that numerous large intercellular spaces exist between them. The light which reaches the spongy parenchyma cells is much less intense than that which falls upon the palisade tissue, for the former are shaded by the palisade parenchyma above them and the light which reaches them from below is, of course, much weaker than that which falls upon the upper surface of the leaf.

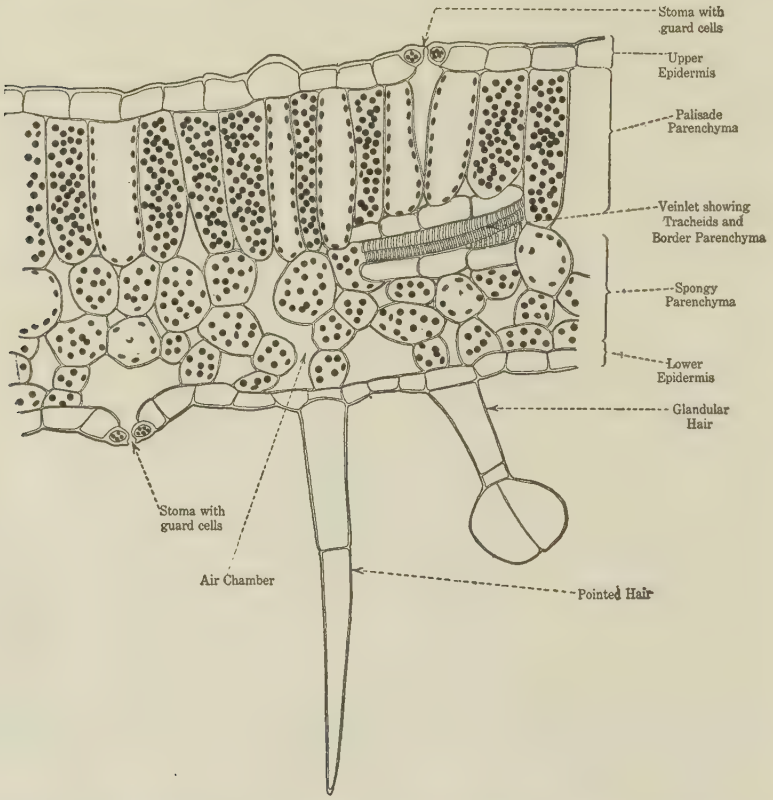


FIG. 88. A cross section of a portion of a leaf of potato (*Solanum tuberosum*). Except for the chloroplasts none of the cell contents have been shown. Some of the cells of the palisade and spongy parenchyma have been shown in section, others in surface view.

The Vascular Bundles.—The vascular bundles which form the midrib, veins, and veinlets not only carry carbohydrates from the green cells, but also conduct water and mineral substances to the mesophyll cells. The mechanical function of supporting the thin expanded sheet of epidermal and mesophyll tissue is performed

principally by the large veins and the midrib, which generally contain considerable quantities of mechanical tissue (fibers, particularly) in addition to conducting tissues (vessels, tracheids, and sieve tubes).

FIG. 89. A "skeletonized" leaf, all the tissues of which, except the vascular bundles, have been removed by decay, leaving the system of veins almost intact, except for the fine, microscopic veinlets.

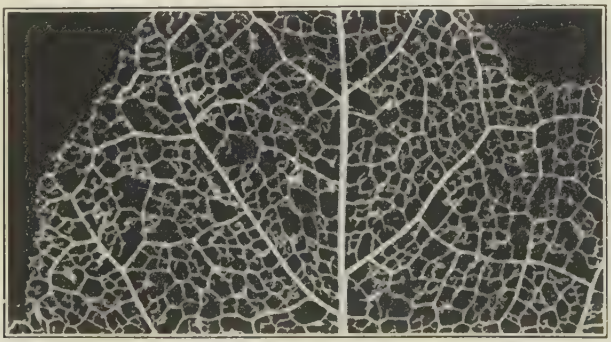


FIG. 90. A portion of a "skeletonized" leaf, all the tissues of which, except the vascular bundles, have been removed by decay, leaving the system of veins. The microscopic "endings" of the bundles and a few of the larger veinlets have been lost.

No cambium is present in the vascular bundles of the leaf. The vascular bundles of the leaf blade continue on down through the petiole and join the vascular tissue of the stem.

Certain important commercial fibers are derived from leaves. Manila hemp is obtained chiefly from the sheathing leaf stalks of the banana-like plant, *Musa textilis*, of the Philippine Islands. Manila hemp is used to manufacture cordage, binder twine, bagging, etc. The leaves of *Agave fourcroydes*, a native Mexican species, yield henequen or Yucatan sisal; the leaves of *Agave sisalana*, a native of Central America and Mexico, ordinary sisal. These agave fibers are made largely into binder twine. Also, the leaves of green aloe (*Furcraea gigantea*) and of New Zealand hemp (*Phormium tenax*) furnish coarse fibers of considerable economic importance.

The Abscission Layer, Leaf Fall, and Leaf Scars.—Leaves of deciduous plants fall to a certain extent at all seasons, but particularly at the approach of winter. The conditions which favor the fall of leaves cause certain cells near the lower end of the petiole to become meristematic and produce a zone of delicate, thin-walled cells extending clear across the base of the petiole. This is called the **abscission layer.** (See Fig. 93.) The middle lamella of these cells becomes changed chemically before leaf fall, and when the wind blows against the blade of such a leaf the cells of the abscission layer separate from one another readily. Certain cells just below the abscission layer become suberized and form a protective layer over the part of the stem from which the leaf has separated. These areas are known as **leaf scars.** Within each leaf scar the **bundle scars,** or broken ends of the vascular bundles which lead from the petiole into the stem, may be seen.

The falling of flowers and fruits, as well as of leaves, is caused by the formation of an abscission layer in the flower or fruit stalk. It has been shown that certain of the growth-promoting substances may delay the abscission of flowers, fruits, and leaves. Practical application of this finding has been the prevention of premature dropping of the fruits of certain apple varieties. Two compounds, namely naphthalene acetic acid and naphthalene acetamide, applied as a very dilute spray to apple trees just before fruit maturity, have caused a much smaller drop of fruit as compared with unsprayed trees.

Photosynthesis, or Carbohydrate Synthesis.—The foods of plants, and also animals, that is, the substances which are capable of being built into tissue and of furnishing the energy needed for any process except photosynthesis, belong principally to the three chemical groups, carbohydrates, fats, and proteins. In the processes of food building, a simple sugar (soluble carbohydrate), glucose, is be-

lieved to be the first carbohydrate compound formed. This sugar is probably the foundation material from which all the other foods, including other carbohydrates (such as starch and cellulose), fats, and proteins are built up. The process of sugar manufacture in the green cells of plants is known as photosynthesis. As stated at the beginning of the chapter, photosynthesis involves the absorption of the energy of sunlight and its accumulation as potential (stored) energy. The raw materials used in the manufacture of glucose are water and carbon dioxide. The green leaf pigment, chlorophyll, absorbs the light energy. Oxygen is the by-product. The important product of the process is the sugar, glucose, but as it accumulates in solution in the mesophyll cells it is changed over into the insoluble carbohydrate starch in which form it remains until darkness interrupts photosynthesis, when it changes again into sugar. Such is a statement, in brief, of the process of photosynthesis. We shall inquire further into the details of this process. But before doing this, let us emphasize again that the green plant alone possesses the power to synthesize carbohydrates from inorganic compounds (simple compounds such as would exist in the world if no plants or animals had ever lived). All non-green plants, such as bacteria, molds, mildews, rusts, smuts, toadstools, etc., and all members of the animal kingdom lack this power, and hence are dependent directly or indirectly upon green plants for their supply of food.

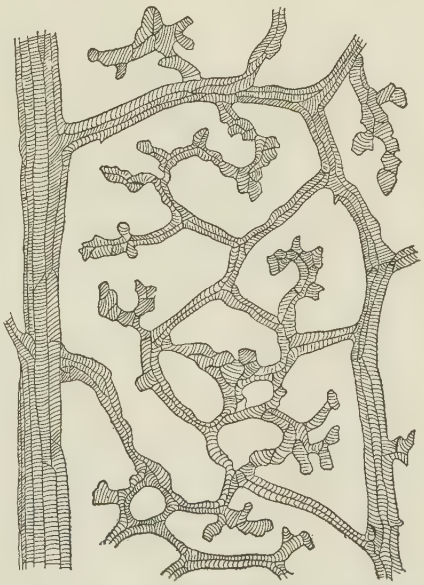


FIG. 91. A portion of the vein system of a leaf. (Redrawn after Sachs.)

Raw Materials.—The soil is the source of the water used in photosynthesis, and the carbon dioxide is absorbed from the atmosphere surrounding the leaves. Although the atmosphere is not absolutely constant in its composition, under natural conditions

the percentage by volume of its principal components seldom varies much from the following figures:

	Per Cent
Nitrogen	78.2
Oxygen	20.8
Argon	1.0
Carbon dioxide	0.03

Traces of ammonia, oxides of nitrogen, ozone, and other gases are also present.

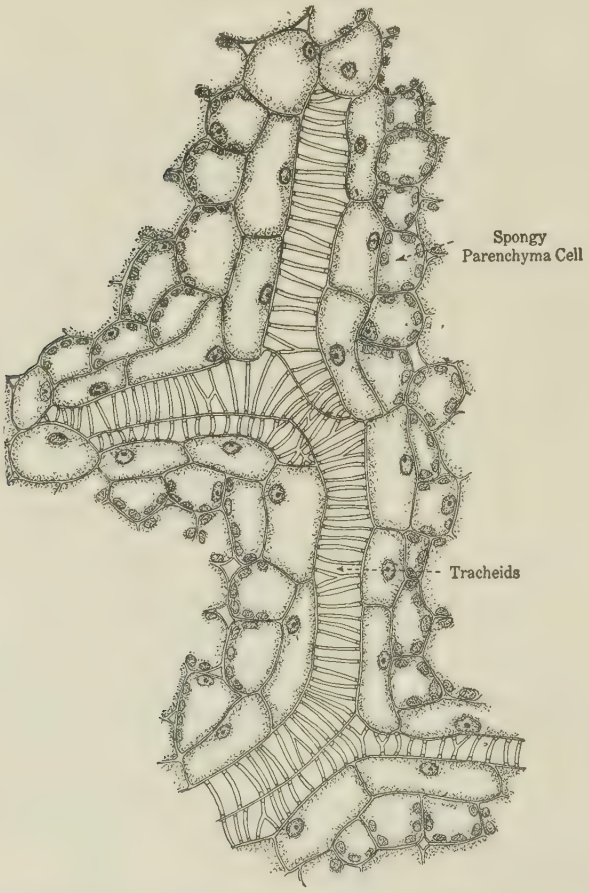


FIG. 92. A section cut parallel to the leaf surface and through the spongy parenchyma. The free ends of several veinlets are shown as well as the relation of parenchyma cells to the finest veins. The tracheids are the spiral type.

Each of these gases is present, therefore, in the intercellular spaces of the mesophyll of the leaf. If the concentration of any one of these gases in the air within the leaf increases, some of that gas will tend to diffuse outward through the stomata. If there is a decrease in concentration of any one of the gases, that gas will tend to diffuse inward through the stomata from the air outside the leaf. The surface film of water on the outside of the palisade and spongy parenchyma cells, where they are in contact with an intercellular

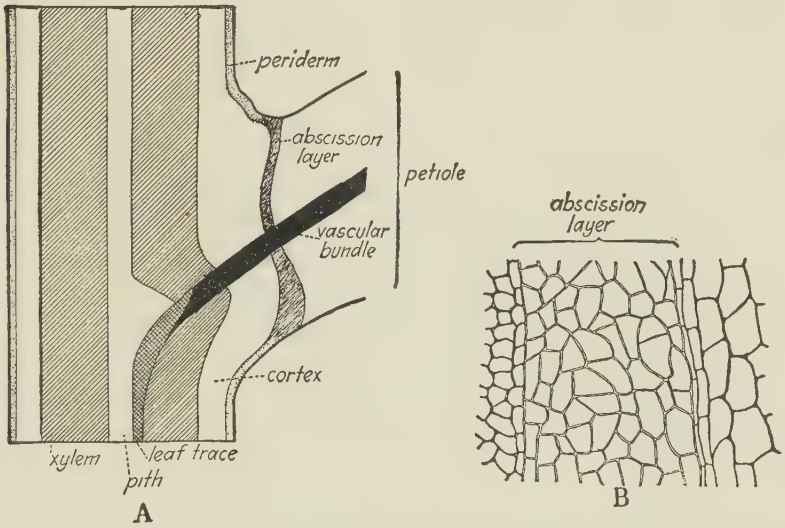


FIG. 93. *A*, diagram showing leaf abscission layer; radial section through twig and leaf base in *Juglans cinerea*. *B*, detail of cellular structure of a small part of the layer three weeks before leaf fall. (From Eames and MacDaniels, *Introduction to Plant Anatomy*, McGraw-Hill Book Company.)

space and the water of the cell wall and cytoplasm, as well as the cell sap of these cells, contains a quantity of each of the atmospheric gases in solution.

During photosynthesis, since carbon dioxide is being taken up from the intercellular spaces by the green cells, there is movement of carbon dioxide from the atmosphere outside the leaf to the interior of the green cells. This transfer of carbon dioxide may be considered as taking place in the following stages:

1. The process of photosynthesis in the chloroplasts removes carbon dioxide from the cell sap of the mesophyll cells. This carbon

dioxide is partly replaced by more carbon dioxide diffusing in from that dissolved in the water permeating the cell wall and forming a water film on the outside of the cells.

2. Solution of more carbon dioxide by the film of water on the surface of the mesophyll cells from the intercellular air, which thus has its carbon dioxide concentration reduced below that of the air outside the leaf.

3. Passage of carbon dioxide from the outside air into the intercellular spaces by diffusion through the stomata.

The water used by the green cells enters the root from the soil and is conducted upward through the xylem of the root and stem. In the leaf it passes through the xylem of the petiole, midrib, and veins to the finest veinlets. None of the green cells is more than three or four cells removed from one of these small conducting strands. Water passes from the tracheids of the veinlets to the parenchyma cells by reason of the much greater concentration of the cell sap of those cells than of the solution (sap) in the tracheids. The process of photosynthesis tends to maintain a high concentration in the cell sap of the green cells, both on account of the sugar which it produces and because of the water which the process removes from the cell sap. But the loss of water by transpiration from the green cells is a much more important factor in maintaining a high concentration in the cell sap of these cells.

The quantity of carbon dioxide and water absorbed and converted into food and tissue by the plant is surprisingly large.

The Energy Factor.—*Necessity of Light for Photosynthesis.*—Experiments show that not only is light absolutely necessary for photosynthesis, but that also the process will not go on unless light actually falls directly on the green tissue. In fact, the chloroplasts themselves must be illuminated. Chlorophyll, as well as carbon dioxide, water, light, and living protoplasm, is essential to carbohydrate manufacture.

The Energy Factor.—*The Function of Chlorophyll.*—What we speak of as white light may be conceived of as consisting of waves of many different lengths, ranging from the relatively long waves of red light, through the successively shorter waves of orange, yellow, and green light to the very short waves of blue and violet light. By means of a glass prism a beam of white light can be

"sorted out" into its different wave lengths and arranged in order according to the length of these waves, the result being what we call a spectrum, or more commonly a "rainbow." When a white object is illuminated by white light, all the different wave lengths are reflected about equally, but, when red light, consisting only of the longest wave lengths visible to the eye, or blue light with its very short waves, falls upon a white object, the object appears to be red or blue because of the reflection to the eye of those wave lengths which fall upon it.

The green color of chlorophyll indicates, at least, that this pigment reflects much of the green component of the white light which

FIG. 94. A "starch print" on a terminal leaflet of scarlet runner bean. The plant was placed in the dark for one day. During this time all the starch previously produced by photosynthesis had disappeared. The leaflet, still attached to the plant, was then covered with tinfoil, from which the letters of the word starch had been cut. After the leaf had been exposed to moderately intense sunlight for several hours it was removed from the plant, killed by placing it in boiling water, treated with alcohol to remove chlorophyll, immersed in a solution of iodine, and then washed. Only where the light fell upon the leaf through the openings in the "stencil" was starch formed. Iodine stains starch blue. Thus the word "*starch*" appeared in dark blue upon the white leaf. A photographic negative may be used instead of a tinfoil stencil and thus portraits or other pictures can be printed upon the leaf.

falls upon it and absorbs (retains) a large part of the light of various other wave lengths which are present in white light. If we pass a beam of white light through a green leaf, the intercellular spaces of which have been filled with water to render the leaf less opaque, and then through a prism, the resulting spectrum will be found to be different from that of white light which has not passed through a green leaf. It will lack a considerable part of the red and much of the blue, indigo, and violet. Another part of the red region of the spectrum and most of the yellow, orange, and green are only slightly

reduced in intensity by passage of the light through the chlorophyll. Thus we learn that it is principally a certain region in the red and a portion of almost all the different wave lengths in the blue, violet, and indigo which are absorbed by the chlorophyll from white light as it passes through the leaf. This is shown by Fig. 95.

The Energy Factor.—*Evidence of the Relative Effectiveness of Different Parts of the Spectrum.*—The production of carbohydrates from carbon dioxide and water is an energy-absorbing process, that is, a process which can go on only if energy is continuously supplied from without. Light is the only form of energy which green plants can use for this process. Now it is clear that the light which the leaf does not absorb cannot be used in photosynthesis, but it

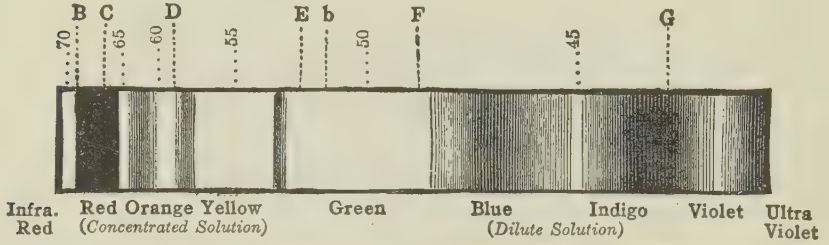


FIG. 95. Diagram of the absorption spectrum of a chlorophyll solution. The numbers give the wave length in hundred-thousandths of a millimeter. The portion to the right is based on the absorption spectrum of a less concentrated solution of chlorophyll than the portion to the left since in a more concentrated solution the three broad absorption bands in the blue, indigo and violet appear as one band. (From Kraus.)

does not follow that the violet, indigo, blue, and part of the red region of the spectrum which are absorbed are all necessarily suitable as sources of energy for photosynthesis, nor does it follow that the relatively small amounts of green, yellow, and orange light which are absorbed cannot be used in photosynthesis. Only experiments can answer the questions as to what part of the absorbed light can be used in carbohydrate manufacture. One of the most direct methods is to project a very brilliant spectrum for some hours upon a leaf which has been freed from starch by being kept for some time in the dark and which receives no other light, and then, after a time, remove the leaf from the plant and treat it successively with boiling water, alcohol, and iodine solution. It will be found that where the orange, yellow, and green light fell upon the leaf there is little or no evidence of starch formation, but that starch is present

where the leaf was lighted by the blue end of the spectrum and by that portion of the red which is most completely absorbed by chlorophyll.

Efficiency of the Leaf in Utilizing Sun's Energy.—It is known that only a portion of the solar energy that falls upon a leaf is utilized in photosynthesis. Some of it is reflected, some is transmitted (passes through the leaf and out the other side), a considerable portion is used in transpiration, and some is converted into heat energy and raises the temperature of the leaf. As a matter of fact, the leaf is very inefficient in its utilization for photosynthesis of the light that falls upon it.

In general, the average efficiency of green plants in the utilization of the sunlight falling upon their leaves is probably as low as 1 per cent, although in some species and under some conditions it may be as high as 5 per cent.

Some interesting estimates of the efficiency of corn plants in utilizing the energy of sunlight have been made by Miller. He found that the maximum daily increase in the dry weight of a single corn plant that had reached its full development was 18.3 grams under field conditions. Assuming that this increase in dry weight was due to starch formation, and that there are 6000 corn plants to the acre, he computed from the heat of combustion of one gram of starch the quantity of energy used for starch formation in one day by an acre of corn. He used for the heat of combustion of starch the value, determined experimentally, of 4200 calories, a calorie being a unit of energy equal to the quantity of heat energy necessary to raise one gram of water one degree Centigrade.

Since the quantity of heat which is liberated when one gram of starch is burned to carbon dioxide and water (heat of combustion of starch) must be equal to the amount of light energy necessary to form that quantity of starch from carbon dioxide and water, then $6000 \times 18.3 \times 4200$ calories, or in round numbers 461,000,000 calories, is the estimated quantity of light energy used per day for starch formation by an acre of corn. This is about $2\frac{1}{4}$ per cent of the whole quantity of energy from the sun falling upon the field during the day.

The By-Product.—Oxygen is given off by the plant during photosynthesis. This gas is an incidental product or by-product of

FIG. 96. A branch of the immersed aquatic plant, *Elodea*, showing the liberation of bubbles of oxygen (a by-product of photosynthesis) when the plant is illuminated.

the process; its production is not to be considered as of any advantage to the plant, for the green cells from which the gas is liberated are in constant and direct contact with the intercellular air of the leaf, which normally contains a large proportion of oxygen. The following equation expresses in simple form the chemical changes which take place during photosynthesis:

$$\underset{\text{(carbon dioxide)}}{6CO_2} + \underset{\text{(water)}}{6H_2O} = \underset{\text{(glucose)}}{C_6H_{12}O_6} + \underset{\text{(oxygen)}}{6O_2}$$

Whereas photosynthesis goes on only during the period of daylight, another important process, respiration, continues during both day and night. Respiration involves the absorption of oxygen and the liberation of carbon dioxide. However, in a green plant which is actively growing and carrying on photosynthesis, the amount of oxygen liberated into the atmosphere by photosynthesis during the daylight hours is very much in excess of that used up by respiration during the whole twenty-four hours. Moreover, the carbon dioxide contributed to the atmosphere by the respiration of such a plant is much less than that absorbed during photosynthesis. It is important to man and to other animals that the concentration of oxygen in the atmosphere be kept fairly uniform in order that their respiration may continue at the accustomed rate. Furthermore, an accumulation of carbon dioxide in the atmosphere would sooner or later interfere with their life process. Therefore, since animals are not able, as

are green plants, to add oxygen to the atmosphere, or to remove carbon dioxide from it, the power of green plants to prevent very great changes in the carbon dioxide or the oxygen concentration in the atmosphere is of considerable importance.

The two processes, photosynthesis and respiration, may be contrasted as follows:

PHOTOSYNTHESIS	RESPIRATION
Its raw materials are carbon dioxide and water.	Its raw materials are glucose, other foods, and oxygen.
It goes on only in cells provided with chlorophyll.	It takes place in all living plant or animal cells.
It takes place only when the cells are illuminated, therefore, in nature only during the day.	It goes on at all times, by night as well as by day.
It is an energy-absorbing process and continues only so long as light energy is supplied to the cell.	It is an energy-releasing process and is independent of energy sources outside the plant.
The energy absorbed is stored in the sugar molecule.	The stored energy of the sugar molecule is liberated in forms, such as heat energy, which are useful to the organism.
Its products are glucose, or other sugars, and oxygen.	When the process goes on to completion its products are carbon dioxide and water.
The gas absorbed during photosynthesis is carbon dioxide, and that liberated is oxygen.	During respiration, oxygen is absorbed and carbon dioxide is liberated.

The End-products.—In most plants the first visible product of photosynthesis is starch. Presumably, glucose is the first carbohydrate produced, but in most plants after considerable glucose has accumulated some of it is transformed to the insoluble carbohydrate, starch, which appears in the chloroplasts as starch grains. In *Vaucheria,* one of the filamentous fresh-water algae, oil is the first product which appears, starch never being formed. In many of the Musaceae (banana family), starch is absent from the leaves, oil being in this case also the first visible product of photosynthesis. In many other monocotyledons there is no visible product of photosynthesis to be found within the green cells, for the sugar produced remains in solution.

As already stated, the sugar which is the immediate product of

photosynthesis has been generally assumed to be glucose ($C_6H_{12}O_6$). This sugar and also sucrose (cane sugar, $C_{12}H_{22}O_{11}$) are present in considerable quantities in most plants.

The Course of the Process.—There have been many attempts to determine the steps by which glucose is built up from carbon dioxide and water. One suggestion which has been put forward is that, from the raw materials (CO_2 and H_2O), formaldehyde (CH_2O) is first formed, and that six such molecules are then built up to form a single glucose molecule ($C_6H_{12}O_6$). It should be stated, however, that the question of the actual course of the chemical reactions involved in carbohydrate manufacture is still an open one.

Rate of Carbohydrate Production.—The amount of carbohydrate produced by a given leaf area in a given time varies greatly in different plants and under different conditions, particularly of temperature and light intensity. In one experiment, the average amounts of carbohydrate produced by pumpkins, cowpeas, and soybeans during a ten-hour period were respectively 1.8, 0.85, and 0.8 gram per square meter of leaf surface per hour. The sunflower (*Helianthus*) may in the course of a summer day produce as much as 25 grams (about one ounce) of starch per square meter (slightly more than a square yard) of leaf surface.

Plants differ greatly in their efficiency in the production of carbohydrates. Most crop plants are relatively efficient in this respect. Man utilizes them because of this. Consider, for example, the sugar beet. One acre of sugar beets, composed of 30,000 individual plants, may produce in a single growing season 5000 pounds of sugar. This is approximately a year's supply for fifty persons. This sugar is manufactured from carbon dioxide and water, with the aid of the sun's energy. No mineral salts of the soil enter into the composition of the sugar molecule. The energy we derive from sugar is in reality transformed radiant energy. Another plant equally efficient in the production of carbohydrates is sugar cane.

Conditions Influencing the Rate of Photosynthesis.—Under natural conditions the rate of photosynthesis is determined by three factors. These are:

1. Temperature.
2. Intensity of the illumination.
3. Carbon dioxide content of the atmosphere.

The lowest known temperature (minimum) at which it is possible for photosynthesis to go on is several degrees below the freezing point of water. For many plants of the temperature zone the optimum (most favorable) temperature for the process is about 37° C., and the maximum (temperature above which the process ceases) 43° to 45° C.

Although, under natural conditions, optimum illumination and temperature exist for considerable periods, green leaves do not, during such periods, produce the greatest quantity of carbohydrates which they are capable of producing, for the 0.03 per cent concentration of carbon dioxide in the atmosphere is far below the optimum. At ordinary temperatures and moderate illumination, artificial increase of carbon dioxide up to a concentration of about 0.25 per cent generally results in increased carbohydrate production. Further increase in carbon dioxide does not increase photosynthesis unless the illumination or the temperature or both are increased.

Under favorable natural conditions of illumination and temperature the carbon dioxide content of the atmosphere is, then, the limiting factor for photosynthesis.

The Utilization of the Product of Photosynthesis.—The sugar, glucose, which is believed to be the first carbohydrate product of the photosynthetic process, constitutes foundation material for the synthesis of many other plant substances. Part of the sugar is respired, liberating energy to be used by the plant in various processes; some of it may be stored as such, or changed into various other plant substances, among which are the carbohydrates: sucrose (cane sugar), starch, and cellulose. All carbohydrates contain the chemical elements carbon, hydrogen, and oxygen. Hence, in the change of glucose ($C_6H_{12}O_6$) to any one of these other carbohydrates, no chemical element is added, there being simply a change in the proportions of the three elements.

Sucrose ($C_{12}H_{22}O_{11}$) is a reserve food, particularly abundant in the root of sugar beet and the stems of sugar cane.

We may speak of "cane sugar" and "beet sugar," but in both cases the sugar is chemically the same, namely sucrose. In 1937-38 the world production of sugar was 34,965,000 short tons. Production of sugar from the sugar cane is heaviest in Cuba, India, Java, Brazil, and the island possessions of the United

States, while the principal countries producing sugar from the beet are Russia, Germany, France, and the United States.

Starch is the most common reserve food in plants. It occurs in nearly all seeds, in roots, and in certain tissues of woody stems. Also, in most leaves it is found as a temporary storage product during the day, accumulating there when the process of photosynthesis proceeds at a greater rate than that of transport of sugar away from the leaf. Cellulose is the principal material of the cell wall. It is the basis of a large number of commercial products such as paper, some explosives, cellophane, celluloid, rayon, etc.

Glucose, or other carbohydrates, may also be converted into fats. In certain plants of the lily family (the onion, for example), oil appears in the leaf cells as the first visible product of food building. In all probability, glucose is, even in these plants, the first product of photosynthesis, but is changed directly into oil instead of into starch as it is in the leaves of most plants.

The fats contain the same elements (carbon, hydrogen, and oxygen) as do the carbohydrates, but the atoms of these elements are very differently arranged in the fat molecules than in the carbohydrate molecules, and the proportion of oxygen is smaller. Fats are especially abundant in the flesh of certain fruits (olive and avocado) and in certain seeds (cotton, peanut, coconut, linseed, etc.) which furnish some of the most important fats and oils of commerce used for soap, cooking, and salad oils, the preparation of paints, and many other purposes.

Glucose also serves as one of the substances from which proteins are built up. In addition to atoms of carbon, hydrogen, and oxygen, very differently arranged than in carbohydrates, all proteins contain the element nitrogen; most of them, the element sulfur; and some of them, the element phosphorus. The nitrogen, sulfur, and phosphorus of proteins are derived from inorganic compounds absorbed from the soil by the roots. Besides being among the most important substances needed for the building up of new protoplasm, the proteins are important storage substances in all seeds, but particularly in such seeds as beans, peas, and cereals. They occur there along with starch, sugar (in sugar corn), and fats.

The basic food is glucose, which is synthesized only in the presence of light and within the chloroplasts. The other carbo-

hydrates, the fats, and proteins are not directly dependent upon light for their formation.

All the wealth produced by agriculture, including not only cereal, fruit, vegetable, and timber crops, but also meat, hides, wool, and other useful materials of animal origin, are directly or indirectly the products of the food-making activities of plants, which in turn are dependent absolutely upon the power of green leaves to absorb the energy of sunlight.

There is a great variety of other substances which, like proteins and fats, are indirect products of photosynthesis, and which may not only play a rôle in the life of the plant, but also yield to man products of great commercial value.

Of the various other substances produced in plants, the following may be mentioned: (1) the **essential oils,** such as lemon oil, cedar oil, clove oil, and other volatile oils which are capable of imparting odors to fruits and flowers and other parts of the plant; (2) the **resins,** found in many plants but particularly abundant in pines; (3) **latex,** a milky secretion (the latex of certain plants is the basis of rubber); (4) various **pigments,** such as chlorophyll, xanthophyll, carotene and anthocyanin; (5) **alkaloids,** nitrogenous compounds, such as quinine (from the bark of the **Cinchona** tree), caffein (from coffee), thein (from tea), morphine (from the poppy); (6) **glucosides,** substances which in decomposition give rise to glucose together with certain other substances (examples of glucosides are amygdalin, which is found in the seeds of the bitter almond and other nuts, and sinigrin, found chiefly in the seeds of mustards); (7) **enzymes,** complex protein compounds, which by their mere presence, even in very low concentration, speed up certain chemical reactions in the plant; (8) **acids,** such as malic acid (from the apple) and citric acid (from citrus fruits); (9) **tannins,** substances which impart an astringent, bitter taste to tissues in which they are present; and (10) **vitamins,** substances which occur in extremely minute quantities in plants and are detectable only through feeding experiments with animals. Animals, including man, are incapable of normal development and maintenance of health if any one of the known vitamins is lacking in their food. Little is known concerning their function in plants.

It is of interest to know that the poisonous nature of certain plants is chiefly due to the presence of either an alkaloid or a glucoside. In the poison hemlock the alkaloid, coniine, is the toxic principle; in death camas, zygadenine; in larkspur, chiefly delphinine. The glucosides are chemical compounds which yield, among other substances, toxic products upon hydrolysis. For example, common sorghum under certain conditions produces a glucoside, dhurrin, which may be hydrolized in the animal's stomach, setting free several products, one of which is prussic acid or hydrocyanic acid, a deadly poison.

The vitamin needs of man are now well recognized. As stated, the majority

of them are obtained directly from plants, or the plant produces substances which, when taken into the animal body, are converted into vitamins. For example, a yellow pigment of plants, carotene, is converted into vitamin A in the animal body. Leafy green vegetables, such as kale, spinach, dandelion greens, watercress, turnip greens, and parsley, and such yellow vegetables as carrots, yellow-fleshed sweet potatoes, and ripe tomatoes are rich sources of the carotenes; these yellow pigments in leaves are always associated with chlorophyll a and chlorophyll b. Milk, butter, and egg yolks contain much vitamin A, which human beings can utilize directly. The cows or hens converted the carotenes which they consumed in feeding into vitamin A. Vitamin B_1, which apparently plays a rôle in the living processes of every plant and animal cell, is manufactured in plants and stored in seeds. It is now synthesized in the laboratory and sold commercially under the name "thiamin chloride." It is used rather extensively to promote root growth. However, not all plants respond to it. There is at present almost complete lack of carefully controlled field trials of the effectiveness of vitamin B_1 under practical conditions; accordingly, it is too early to say definitely that it will find a place in horticultural practice. Vitamin C is best known as the scurvy-preventing vitamin. Some animals, such as cattle, swine, and poultry, manufacture their own vitamin C, but many must get it in their food. Green vegetables and citrus fruits are well-known sources of this substance. Vitamin D, the substance which aids the body in its assimilation of calcium and phosphorus and thus helps make bones and teeth, is derived from sterols acted upon by ultraviolet light. Sterols occur in all natural foods. Other well-known vitamins are vitamin E and vitamin G (riboflavin), which occur widely in common foods.

By the way of summary we may say that food building in the green plant is a series of chemical changes, involving the transformation of energy and the construction of certain complex compounds from simple raw materials absorbed from the soil and the atmosphere. The initial process is that of glucose synthesis from carbon dioxide and water, a process carried on in green cells in the presence of light. In this process the plant absorbs light energy. In fact, photosynthesis and transpiration are the only processes in the green plant in which energy received from outside the plant is utilized. All other chemical changes in the green plant which involve energy probably employ energy liberated within the plant's body, by the process of respiration. With glucose as a basis, plants construct scores of different substances, some of which are of great economic importance. Most of these play a part in the life of the plant; others appear to be waste products or by-products.

TRANSPIRATION

The plant is constantly losing water to the atmosphere. This water comes from the soil, enters through the roots, moves in the conducting tissues to the leaves, and escapes as vapor from the moist cell walls of the mesophyll into the intercellular spaces, from which it passes by diffusion through stomata, and to a much less extent through the cuticle, to the atmosphere. There is such loss of water from the young stems also, in fact from the entire surface which is exposed to the air, although the quantity lost from the surface covered with bark is very little. That leaves lose water may be readily demonstrated by taking an actively growing potted plant, covering the pot and soil with rubber cloth or oiled paper so that no moisture can escape from the surface of the pot or soil, and then placing the potted plant under a bell jar. Afer a while, water will have accumulated on the inner surface of the bell jar; this water could have come only from the surface of the plant. The loss of water in the form of vapor from a living plant is called **transpiration**. Transpiration goes on both day and night, but is generally more active during the daytime than at night. The total amount of water lost from plants during a growing season is enormous. Thus it has been shown that a single corn plant may lose during its growing season as much as 54 gallons of water, and that a corn plant that has reached its full development may evaporate each day a quantity of water equal to twice the weight of the plant. Under the conditions of relatively high temperature and low humidity surrounding most actively growing plants, this great

FIG. 97. Photograph of a rose leaf showing water of guttation adhering to the "teeth" around the margins of the leaflets.

loss of water is unavoidable because of the structure of the leaf, which, although well adapted for the absorption of carbon dioxide and the escape of oxygen gas, involved in photosynthesis, cannot prevent the simultaneous loss of water vapor. Moreover, the amount of surface exposed by the leaves of a single plant may be surprisingly large. For example, the combined surface exposed by the leaves and sheaths of a well-developed corn plant may amount to 30 to 35 square feet, which is from four to six times as great as the soil surface on which the plant is growing. It is stated that a wild sunflower plant growing under favorable conditions may have a total leaf surface of as much as 40 to 50 square feet. Such figures make it easy for us to believe what many experiments have shown, that the quantity of water lost from a given area of soil by the transpiration of the plants growing upon it often greatly exceeds that which would be lost directly from the soil by evaporation if the plants were removed.

In the semi-arid agricultural sections it is common practice to plant small cereals every other year on a given area. As a rule, the water stored in the soil from one season's rainfall is insufficient to grow a profitable crop of grain. In alternate years the soil is "fallowed," i.e., it is uncropped and cultivated frequently enough to keep down all plant growth. By this practice, loss of water from the soil by transpiration is eliminated. The only water loss is that of evaporation from the soil surface, which loss may be decreased by mulching the surface. It is now recognized that the principal injury of weeds in a cultivated crop is their use of soil water; or, in other words, the chief reason for cultivating is the elimination of weeds which, through transpiration, remove water from the soil.

Conditions Affecting Transpiration Rate.—The amount of water lost by transpiration is influenced by a number of factors, chief of which are the following: (1) the structure of the leaf; (2) light; (3) the evaporating power of the air, which depends upon temperature, relative humidity, and wind; and (4) the water content of the soil. Thus, we see that the rate of transpiration depends upon certain internal factors, that is, conditions in the plant itself, and also upon certain external factors.

Leaf Structure.—Although the loss of water from the leaves is large, leaf structure is such that it does regulate somewhat the escape of moisture. The principal means by which the plant is able to reduce cuticular transpiration are the thickening of

the outer wall of the epidermal cells, the presence of large quantities of the wax-like material, cutin, in this wall, and the production of close-set rods of wax (the so-called "bloom" which occurs on many fruits, leaves, and stems, and has the appearance of a very fine

FIG. 98. A potometer for measurement of the rate of transpiration. Withdrawal of water from the apparatus by the leafy shoot to make up for that lost by transpiration causes water to move from left to right in the horizonal capillary tube. This tube is bent downward near the end and dips under the water in the vial shown at the left, from which it draws water through its open end. If the tip of the capillary tube, which is graduated in 500ths of a cubic centimeter, is raised for a few seconds above the surface of the water in the vial an air bubble enters the tube. The distance moved by this bubble in a given time shows the rate of transpiration. By turning the stop cock at the base of the perpendicular water reservoir the bubble can be forced back to its original position after each observation. A potometer with larger receptacle for the plant so that a small plant with its entire root system can be used is preferable to the apparatus shown. Above, a portion of the capillary tube, slightly magnified, showing a bubble between the fifth and ninth graduations.

powder). Some water is lost through the cuticle of a leaf, but it is generally only a small fraction of that which passes out through the stomata. For example, in an ivy leaf the transpiration during

the day through the cuticle may be no more than one-thirtieth of the total transpiration.

In many plants the stomata are largely or entirely confined to the lower surface of the leaf. Clearly stomata on the under surface of the leaf will be less likely to endanger the plant by allowing excessive transpiration than would stomata on the upper surface. The temperature of the lower, and therefore shaded, side of the leaf will be less than that of the upper side when the sun is shining brightly, and consequently the air adjacent to the lower surface of the leaf will not tend to be so dry as that next to the upper surface of the leaf. One might suppose from the great number of stomata on the leaves (as many as 428,000 per square inch of leaf area in the cucumber, or from 50,000,000 to 60,000,000 on a single fully developed pumpkin leaf) that they occupy a relatively large proportion of the epidermal surface of the leaf. As a matter of fact, the combined area of the stomata (the actual openings) in such cases is 1 to 3 per cent of the total surface of the leaf.

Leaves which hang straight down, like those of some poplars and the adult leaves of eucalyptus, have about the same number of stomata on the two sides. The same is true of leaves which stand almost or quite perpendicular, as in many grasses. In the case of a few plants, such as those water-lilies whose leaves float on the surface of the water, there are no stomata on the lower surface of the leaf.

In general, it may be said that leaves reduce water loss by closing the stomata whenever there is no necessity for carbon dioxide absorption. The guard cells generally react promptly to a change from light to darkness or from darkness to light, closing the stoma in the former case and opening it in the latter, but the stomatal behavior of some plants is not easy to explain. There are some plants like the willows which are unable to close their stomata.

When water shortage begins, certain plants, particularly grasses, reduce both stomatal and cuticular transpiration by rolling of the leaves. By this method the amount of leaf surface exposed to light and to the dry atmosphere is decreased.

It is commonly assumed that the presence of epidermal hairs reduces transpiration. Of this there is some question, especially if the hairs are made up of living cells.

Many plants living in places where the water supply in the soil is small and the atmosphere very dry appear to have reduced transpiration, both stomatal and cuticular, by having very small leaves, by shedding the leaves soon after they are formed, or by producing no leaves at all. In either of the two latter cases the stems perform the typical leaf functions. Clearly such provisions for restricting water loss result in a great sacrifice of photosynthetic activity.

FIG. 99. Leaf spines of common barberry (*Berberis vulgaris*). A short shoot bearing ordinary foliage leaves stands in the axil of the branched spine-like leaf.

Light. — Illumination has a marked effect on water loss by transpiration. Illumination increases transpiration in the following ways: (1) by raising the temperature of the surrounding air, and (2) by causing the guard cells to open the stomata.

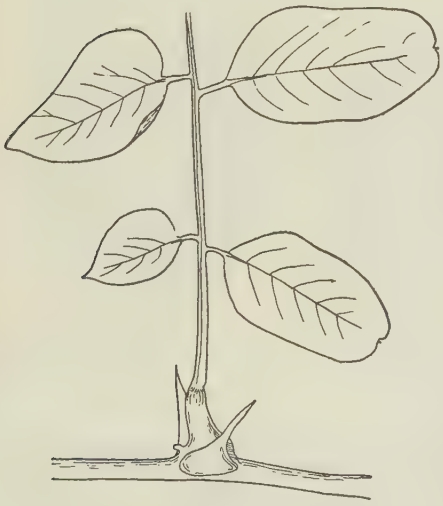


FIG. 100. Stipular spines of black locust (*Robinia pseudacacia*).

The Evaporating Power of the Air.—The lower the relative humidity of the air surrounding the plant, the greater the transpiration will tend to be. Though transpiration is very slight in a water-saturated atmosphere, it has been shown that it does not cease entirely. When the air surrounding the plant is quiet, it becomes almost saturated with water vapor because of transpiration and the slowness with which the water vapor diffuses away

from the leaf. This "moist blanket" of air naturally checks transpiration. Movement of the air sweeps away the mantle of moist air and brings fresh and drier air to the surface of the leaves.

Water Content of the Soil.—In general, if other factors are the same, transpiration is at a maximum when there is an abundance of water in the soil, and transpiration decreases when the water content of the soil is reduced to the point where wilting (not permanent wilting) begins. The transpiration rate of a turgid plant greatly exceeds that of a wilted one. Consequently, any soil condition which brings about wilting, even incipient wilting, will reduce the transpiration rate.

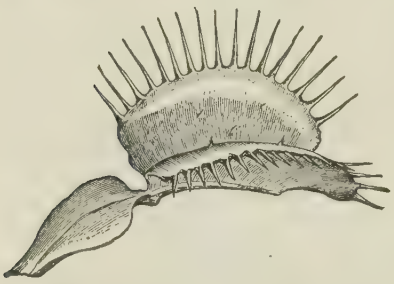


FIG. 101. A leaf of Venus' Flytrap (*Dionaea muscipula*) an insectivorous plant. (After Darwin.)

Autumnal Coloration of Leaves.—The brilliant yellow and red tints which the leaves of deciduous trees, such as maples

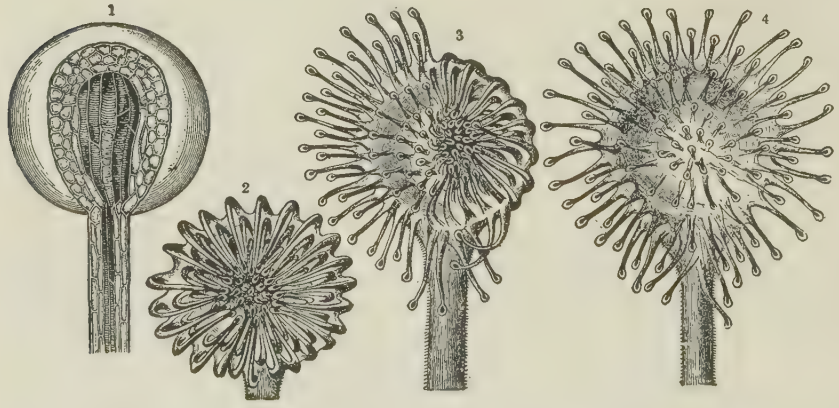


FIG. 102. Sundew (*Drosera*), an insectivorous plant. The leaves are covered with "tentacles" (4) each of which (1) bears a gland at the tip from which a viscid fluid is secreted. Insects often come in contact with the sticky tentacles and are held, in which case neighboring tentacles bend over until they are in contact with the captured insect (3). All the marginal tentacles may respond (2). The result is that the insect becomes engulfed in the sticky secretion and is in part digested by an enzyme contained in this secretion. It is probable that the plant is able to utilize the nitrogenous food thus secured to supplement the relatively limited supplies of inorganic nitrogen available in the soil of the particular localities in which such plants are native. (After Kerner.)

(*Acer*), may assume some time before their fall, and which contribute so much to the beauty of the woods in autumn, are due to chemical changes which take place in the leaf. Yellow colors result from the decomposition of chlorophyll without alteration of xanthophyll and carotene, and the red colors are due to the formation of a

FIG. 103. Pitchers of four insectivorous plants. A, *Sarracenia variolaris*. B, *Darlingtonia californica*. C, *Sarracenia Drummondii*. D, *Nepenthes villosa*. (After Kerner.)

pigment, anthocyanin, from sugars and certain products resulting from the disintegration of chlorophyll.

Special Functions Sometimes Performed by Leaves.—Besides the primary functions of photosynthesis and transpiration, and those of growth and of respiration (which is constantly going on in the cells of the leaf as in all living cells of the plant), the leaves of various plants may perform certain special functions in

the service of the whole plant. In some cases the leaves that are adapted to carry on such special functions continue actively to transpire and to manufacture food, but in others their adaptation to perform a special rôle in the life of the plant is attended by loss of the primary functions. Examples of such special functions are protection (bud scales and leaf spines), food storage, water storage, attachment (tendrils), and capture of insects (by insectivorous plants). The rudimentary foliage leaves of most perennial woody plants (of cold and temperate regions) and the other parts within the buds are protected by scale leaves called bud scales. These are generally small, brown in color, and rather tough in texture. They are often densely covered with hairs on the outer surface. A good example of a plant in which the leaves have been transformed into protective spines is the cactus. The bulk of such bulbs as the onion (*Allium*) is made up of special food-storage scale leaves. Plants of dry soil or salt-marsh habitats often have leaves much thickened and provided with a very efficient cuticle which enables them to store a great quantity of water. Leaves or leaf parts, as petioles or stipules, may be modified into tendrils. Insectivorous plants have their leaves modified in various ways to capture insects. See Figs. 101, 102, and 103.

In the absence of leaves the leaf functions are sometimes taken over entirely by other organs, by the roots, for instance, in some tropical orchids, or by the stems, as in Scotch broom and asparagus.

CHAPTER VII

THE FLOWER

An individual plant functions not only for itself but also for the species to which it belongs. Up to this point we have discussed those plant organs—roots, stems, leaves—which are concerned primarily with the vegetative activities of the plant, i.e., with those activities or functions through which the individual plant provides for its own needs. It will be recalled that the chief of these functions are absorption, conduction, manufacture of foods, assimilation, growth, transpiration, and respiration.

The function of reproduction has nothing to do with the welfare of the individual plant which performs it. In fact, in many plants reproduction is always a forerunner of the death of the parent plant. For example, in annual plants, very soon after the formation of flowers and seeds, the vegetative organs wither and die. Only the seeds persist. The reproductive function, by the origin of new individuals, serves to prevent the extinction of the species, to multiply the number of plants of the species, and to distribute the species over a larger area.

In the seed plants, which include most cultivated plants, the flower is the organ of sexual reproduction. Sexual reproduction is fundamentally the same in all organisms in that it involves the union of two specialized reproductive cells, called **gametes**, to form a single cell, the **zygote**, which develops into the new individual. It is in the flower that these reproductive cells are produced, their union effected, and the new individual developed (within the seed).

We should keep in mind, however, that not all reproduction, even in the seed plants, is by sexual means. Many common plants reproduce without sex, that is, **asexually**, or without formation and fusion of gametes. Cuttings of stems of many plants will develop roots and grow into complete plants if kept in moist soil. Leaves

of some species of *Begonia* will produce new plants if kept in close contact with moist soil. Potato tubers and lily bulbs are also special asexual reproductive structures.

In size, form, arrangement, odor, and color, flowers show an almost infinite variety. The flowers of the duckweed, a floating aquatic plant, are so minute that they are not easily seen with the naked eye, whereas a single flower of the tropical *Rafflesia* some-

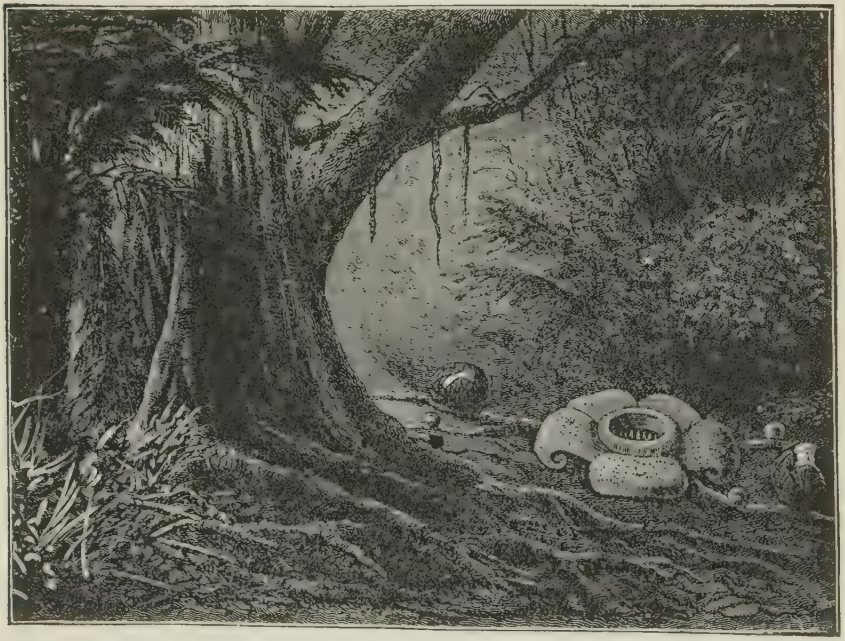


FIG. 104. A giant flower, almost a meter in diameter, and several flower buds of the tropical parasite, *Rafflesia*. Leaves, roots and stems are lacking. Aside from the flowers, and the fruits which develop from them, the entire plant body of the parasite consists of tissue buried within the root of the host and absorbing food from it. (After Kerner.)

times measures 3 feet across. We are quite familiar with the remarkable variations in flower form and color; a visit to any conservatory or a trip to the field reveals these variations.

Flowers owe their fragrance chiefly to volatile oils. Some flowers, those of the poppy, for example, are odorless; most flowers, however, have a pleasant scent, but a few, such as those of skunk-cabbage, have an extremely repulsive odor.

A knowledge of the structure of the flower and of how its parts function is necessary to an understanding of many practical problems involved in the growing of plants, such as the following: Why do blossoms often fail to set fruit? How are artificial pollination and the hybridizing of plants accomplished? What are the causes of misshapen fruits? What are the causes of seedless fruits? What are the relations of flower structure and of pollination to insects?

STRUCTURE OF THE FLOWER

In most flowers there are four principal kinds of flower parts, which, taken in order from the outside to the inside of the flower, are as follows:

1. The **sepals** (together called the **calyx**), which are usually green, and enclose the other flower parts in the bud.

2. The **petals** (together called the **corolla**), which are usually the conspicuously colored portions of the flower.

3. The **stamens**, each made up of an **anther** (pollen-bearing body), borne at the top of a **filament** or stalk.

4. The **pistil**, consisting of: (1) the **ovary** (a swollen basal portion which becomes the fruit); (2) the **style** (a slender column of tissue which arises from the top of the ovary and through which the pollen tubes grow); and (3) the **stigma** (expanded tip of the style to which the pollen adheres).

The petals and sepals taken together are called the **perianth.** The **receptacle** is the broadened end of the flower stalk to which the floral parts are attached. The **peduncle** is the name applied to the stalk of a flower which is borne singly, or to the stalk of a flower cluster (**inflorescence**). The branch stems bearing the individual flowers of a cluster are called **pedicels.**

In a typical flower the center is occupied by the pistil or pistils; in a circle or **whorl** surrounding these are the stamens; outside the stamens is a circle of petals; and surrounding these a whorl of sepals.

Pistils and stamens are essential to reproduction; without the cooperation of both, seed cannot be formed. Petals and sepals are not essential but perform secondary functions; they protect

the essential parts in the bud and attract insects, which in many flowers are needed to bring about the transfer of the pollen to the stigma, which is necessary for seed production.

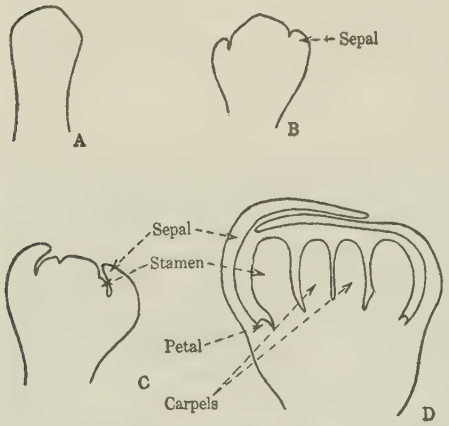


FIG. 105. Origin and development of flower parts of shepherd's purse (*Capsella*). *A*, apex of the floral axis before the appearance of the primordia of any of the flower parts. *B*, appearance of sepals. *C*, the stamens have made their appearance and the carpels are just beginning to form. *D*, the petals have appeared and the primordia of the carpels also. Note that the latter in their formation involve all that remains of the promeristem of the floral axis. (Redrawn from Coulter and Chamberlain.)

Examination of a flower shows that it is really a shoot, for it is a stem, generally a branch one, bearing leaves (the flower parts) which are specially adapted to carry on reproduction. For this reason these floral leaves are very different from foliage leaves. The flower has its origin in the axil of a leaf, just as does an ordinary branch. The leaf which thus subtends a flower is ordinarily quite unlike a foliage or floral leaf, and is called a bract. Though really a branch, the flower differs from branches bearing foliage leaves in the following three important particulars:

1. The promeristem of this branch does not continue to grow, but is completely used up in the formation of the floral leaves.

2. The floral leaves, instead of being separated by clearly perceptible internodes, are crowded together.

3. Normally there are no buds in the axils of the leaves which compose a flower.

Sepals.—In the flower bud the petals, stamens, and pistils are usually enclosed within the calyx. This protects the parts within from mechanical injury, from rain, and from drying out. In accordance with the protective function which they serve in the bud, the sepals are generally of firmer texture than the other flower parts. However, when the petals are lacking, as in *Clematis*, the sepals, instead of being relatively small, green, and leaflike, may become large,

delicate, and highly colored structures, very similar to typical petals and performing the function of petals.

Petals.—In most flowers the petals probably attract insects which carry pollen from the stamens of one flower to the tip of the pistil (stigma) of another. This transfer of pollen from the stamen to the stigma is essential to seed formation. The petals may attract insect visitors not merely by their large size and conspicuous coloration, but

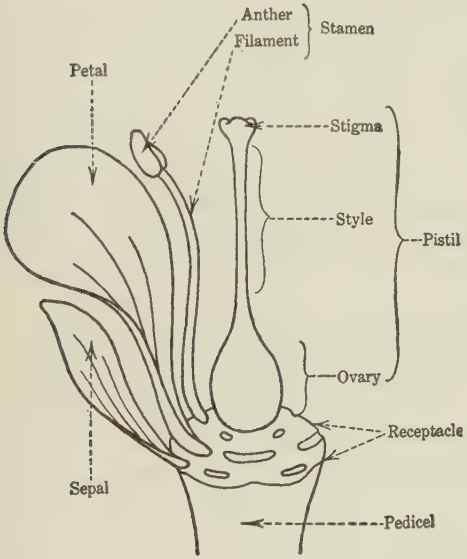


FIG. 106. Diagram of a flower from which all but one member of each whorl of flower parts have been removed. (Based on a figure in Hall's *A Yosemite Flora.*)

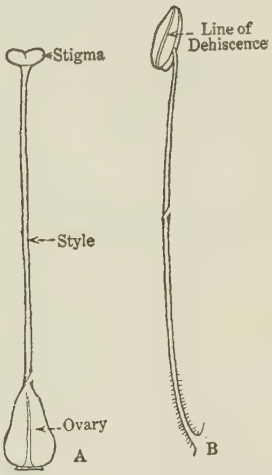


FIG. 107. The essential flower parts of tobacco (*Nicotiana*). *A*, the compound carpel consisting of two carpels. *B*, a stamen, showing the filament (stalk) and anther.

frequently, also, by the perfume which they produce, and often by the sweet product (nectar) of their sugar-secreting glands or nectaries.

The color of the petals may be due (1) to pigments dissolved in the sap of their cells, (2) to pigments contained in the plastids, or (3) to the combined effect of both kinds of pigmentation.

Stamens.—The stamen consists of a filament and an anther. The filament serves merely to support the anther; the anther performs the essential function of the stamen, which is pollen production. The anther consists of two lobes, elongated in a longitudinal direction, and united by a band of tissue called the connective. If

an unripe anther is cut crosswise it can be seen that each lobe contains two cavities, or **pollen sacs**, within which the pollen grains are produced. When the pollen is ready to be shed the pollen sacs generally open by longitudinal slits.

Stamen filaments are plant structures which may grow very rapidly. For example, in the flower of wheat, the filaments may grow 2 to 3.5 millimeters per minute.

Pistils.—The pistil is believed to consist of one or more units, each of which is a modified seed-bearing leaf, known as a **carpel.** A carpel with its edges united, or several carpels with their edges joined, forms the **ovary** which encloses the ovules. When a pistil consists of a single modified leaf or carpel, it is spoken of as a **simple pistil,** as, for example, in the bean or pea flower. When a pistil is composed of several united leaves or carpels, as in the flowers of lily, onion, potato, etc, it is said to be **compound.** A cross section of a

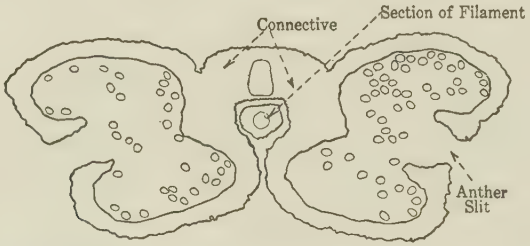


FIG. 108. Cross section of an open anther of lily (*Lilium*). Note that the walls separating the two pollen sacs of each anther lobe (*theca*) have broken down so that but one chamber now exists in each half of the anther.

compound pistil, cut through the ovary, usually shows two or more compartments or chambers.

Whether the pistil is simple or compound, it almost always has three parts: (1) an enlarged basal part called the **ovary,** which is just above the attachment to the receptacle; (2) a column of tissue arising from the top of the ovary and called the **style**; and (3) a more or less expanded part at the upper end of the style, called the **stigma.** The stigma commonly has its surface roughened by short, cellular protuberances, and sometimes secretes a sticky solution, the stigmatic fluid. This roughened surface of the stigma, together with the stigmatic fluid when present, facilitates the adherence of pollen. In wind-pollinated plants, grasses for example,

the stigma is often much branched, which fits it to catch the pollen carried by the air. The style may be very short or even lacking, or long and filamentous as the styles (corn silk) of Indian corn.

The regions within the ovary to which the **ovules** (potential seeds) are attached are known as **placentae** (singular, **placenta**).

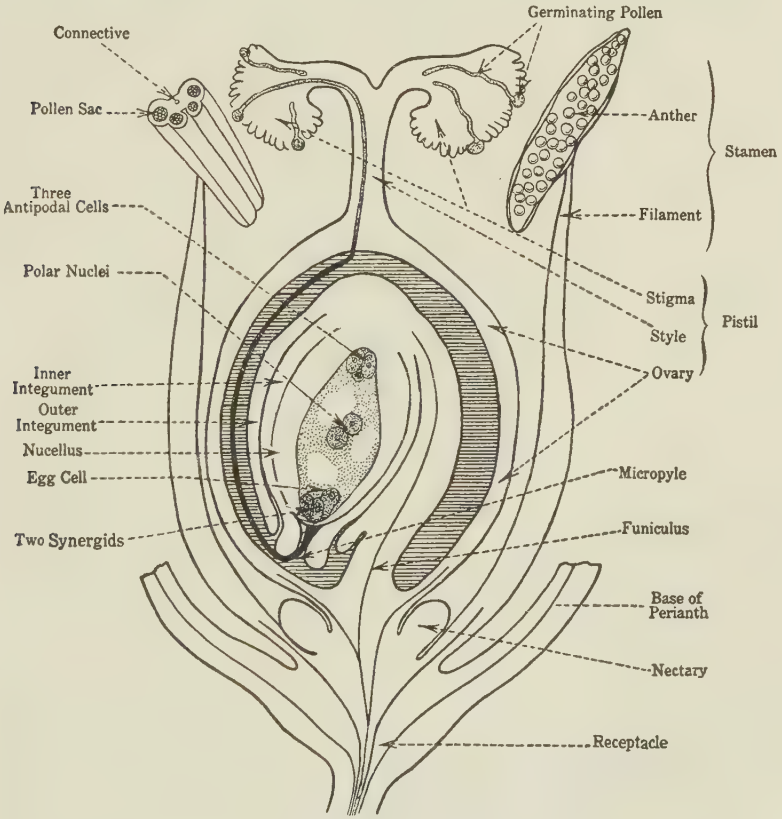


FIG. 109. Diagrammatic longitudinal section of a flower. (Redrawn from Sachs.)

In most flowers the number of placentae is the same as the number of carpels in the pistil, and in such cases the placentae generally correspond quite evidently to the inrolled and united edges of the carpels.

The mature ovule consists of the following parts (Figs. 109 and 110): (1) a **stalk** which attaches the body of the ovule to the placenta, (2) **integuments**, layers of tissue which surround (3) a

mass of tissue, the **nucellus**, within which is (4) the **embryo sac.** The embryo sac is a structure of great importance in the process of sexual reproduction whereby the ovules become transformed into seeds. A more detailed description of the embryo sac will be given later in the discussion of the process of seed formation.

Incomplete Flowers.—A great many species of plants are lacking in one or more of the four kinds of flower parts present

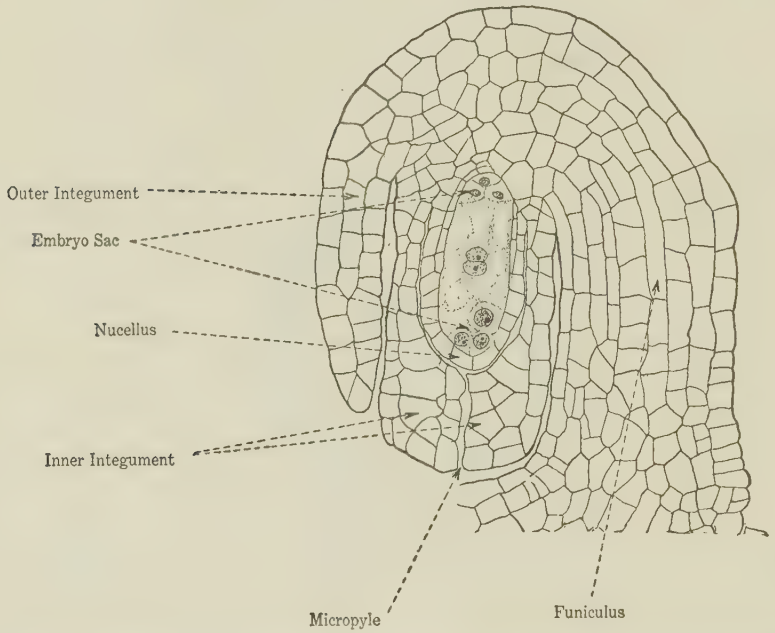


FIG. 110. Longitudinal section of a lily (*Lilium*) ovule showing the embryo sac ready for fertilization. At the end of the embryo sac nearest to the micropyle are the two synergids and the egg cell; at the opposite end are the antipodal cells and in the center are the polar nuclei.

in typical flowers. In the buckwheat flower, for example, the petals are absent. In the flowers of willows and cottonwoods both sepals and petals are lacking. In both of the foregoing cases the essential organs (stamens and pistil) are present. However, some plants have but one set of essential organs—either stamens, or a pistil—in any single flower. A flower with stamens only, and no pistil, is said to be **staminate** (male). On the other hand, a flower with a pistil but no stamens is called a **pistillate** (female) flower. In such cases,

the staminate flowers do not produce fruit and seed. Staminate and pistillate flowers may be on the same individual plant; this is true of corn, in which the "tassel" is a group of staminate flowers, and the "ear" a group of pistillate flowers. Such plants are said to be **monoecious.** The squashes, pumpkins, and melons are other examples of monoecious plants. Staminate and pistillate flowers may be on different individual plants; examples of such plants are

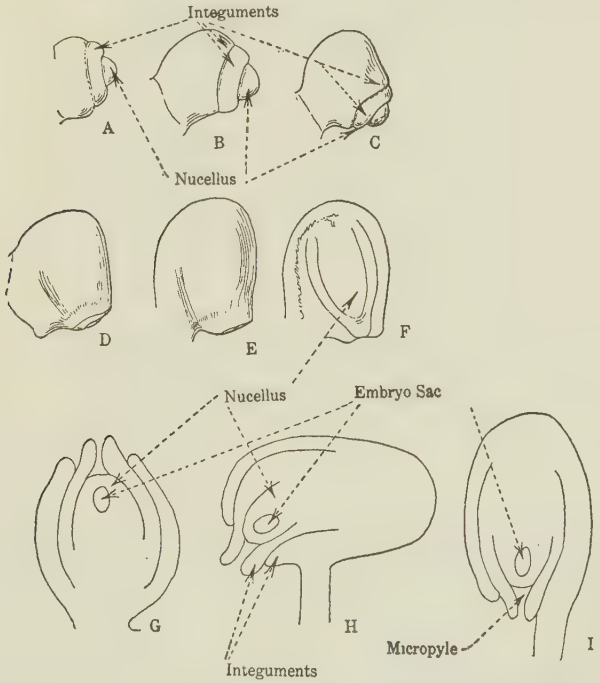


FIG. 111. *A-F*, stages in the development of an ovule; *G-I*, three types of ovules differing in the attachment to the stalk or funiculus. (*A-F*, redrawn from Gray; *G-I*, redrawn from Prantl in Engler and Prantl's *Nat. Pflanzenfam.*)

asparagus, spinach, hops, willows, and date palm. Such plants are said to be **dioecious.** In these plants the flowers on any one plant are either all staminate or all pistillate. Thus we may speak of staminate (male) plants and pistillate (female) plants.

In certain cultivated dioecious species, one of the two kinds of plants may be more desirable from the grower's standpoint than the other. For example, in the date palm, it is desirable that most of the individuals be pistillate since these alone bear fruit. In the hop

plant, it is only from the pistillate plants that the "hops" are obtained. In asparagus, it has been found that the yield of edible spears from staminate plants exceeds that from pistillate.

Form and Arrangement of the Parts of Flowers.—The majority of flowers are typically star-shaped, that is, they have a corolla

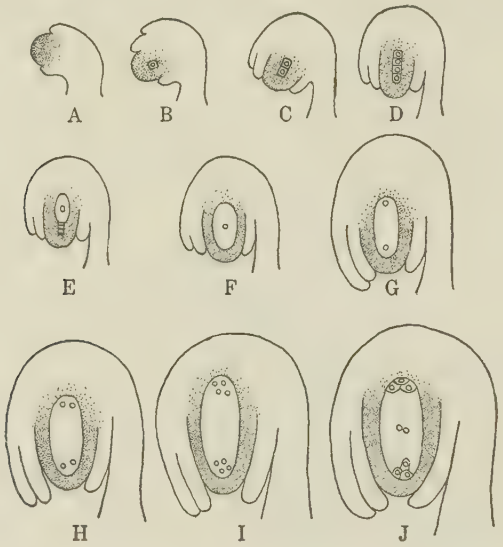


FIG. 112. Stages in the development of an ovule, showing the origin and growth of the integuments and the formation of the embryo sac. *A*, inner integuments beginning to grow up about the nucellus. *B*, outer integuments are appearing. The continued growth of these integuments is shown in the figures which follow (*C-J*). *B*, the embryo sac mother cell which has developed from one cell of the nucellus. The nucleus of this one cell has the "2*n*" number of chromosomes. *C*, the embryo sac mother cell has undergone one division (the reduction division), to form two cells, each with "*n*" number of chromosomes in their nuclei. *D*, each of the two preceding cells has divided, resulting in a row of four cells imbedded in the nucellus. *E*, three of the cells (the ones nearest the micropyle), degenerate and disappear, whereas the basal cell of the four enlarges greatly. *F*, embryo sac with one nucleus which has "*n*" chromosomes. *G*, 2-nucleate embryo sac. *H*, 4-nucleate embryo sac. *I*, 8-nucleate embryo sac. *J*, mature embryo sac, with 2 synergids cells and 1 egg cell at the micropylar end, 2 polar nuclei near the center, and 3 antipodal cells.

composed of similarly shaped and equally spaced petals which radiate out from the center of the flower. Flowers of this type almost always have a similar arrangement of the other flower parts and are usually regular flowers in that all the members of each whorl are of the same form. Such a condition in a flower or any other structure is often spoken of as radial symmetry. There are,

however, many flowers which are not "star-shaped" and generally in these one or more members of at least one whorl are of different form from the other members of the same whorl. Among the most familiar examples of such **irregular** flowers are the blossoms of peas, beans, and most other Leguminosae, and of violets. Flowers such as these do not have radial symmetry, but at the most, **bilateral symmetry**, which is to say that there is only one plane along

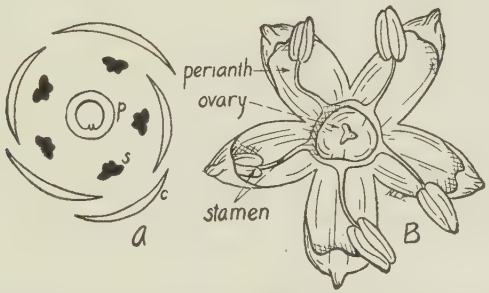


FIG. 113. Incomplete flower of beet (*Beta vulgaris*), which has a calyx but lacks a corolla. *A*, floral diagram. *B*, face view. (After Robbins, from *Botany of Crop Plants*.)

which they can be cut into halves that are mirrored images of each other.

Hypogyny, Perigyny, Epigyny.—When the receptacle is convex or conical, the whorls of flower parts are situated one above another and in the following order, beginning with the lowest: sepals, petals, stamens, and carpels. Such a flower is said to be **hypogynous.** When the receptacle is a more or less deeply concave structure, at the center of which is the pistil and at the margins of which are the sepals, petals, and stamens, these parts seem to be attached around, instead of below, the ovary, and the flower is called **perigynous.** The ovary of a perigynous or hypogynous flower is spoken of as **superior.** If the concave receptacle not only surrounds the ovary but is also fused with it so that the other flower parts appear to arise from the top of the ovary, the flower is **epigynous,** and the ovary is said to be **inferior.** The fruits formed by epigynous flowers often bear at the unattached end the withered remains of the sepals and stamens or of other flower parts. The cherry, peach, and plum (species of the genus *Prunus*) have perigynous flowers; and the apple and pear have epigynous flowers.

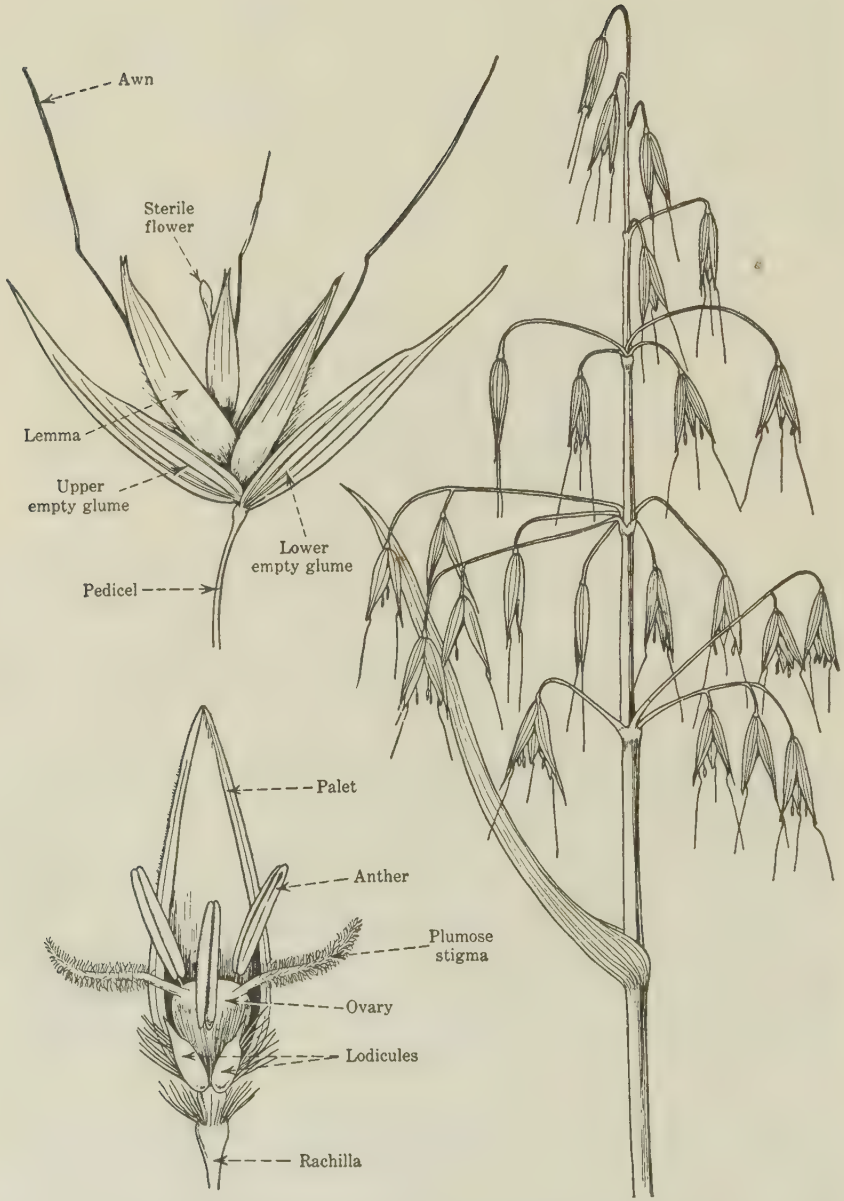


FIG. 114. Wild Oats (*Avena fatua.*) (Right)—the inflorescence, a panicle. (Upper left)—a single spikelet with three fertile flowers and one sterile flower. (Lower left)—a single flower. (After Jepson, from *Flora of Economic Plants.*)

Pollination.—As was stated earlier in this chapter, the anthers of the stamens open when the pollen is mature, and the pollen grains escape. The transfer of the pollen from the anthers to the stigma is called **pollination.** The pollen is carried chiefly by wind and insects. Such inconspicuous flowers as those of grasses, willows, alders, oaks, and pines are examples of those which have their pollen dispersed by the wind. It is of interest to note that, as a rule, plants

FIG. 115. The imperfect flowers of field pumpkin (*Cucurbita pepo*). *A*, staminate flower. *B*, pistillate flower. (After Robbins, from *Botany of Crop Plants.*)

whose pollen is likely to cause hay fever are chiefly wind-pollinated species. Fruit trees are largely dependent upon insects for the dispersal of their pollen.

In grasses the flowers are inconspicuous. They lack odor and nectar, and hence are not attractive to insects; furthermore, the pollen is light and dry, and easily carried by the air; the stigmas are feathery and expose a large surface to flying pollen; and the pollen is often produced in great quantities. For example, in Indian

corn it is estimated that each group of staminate flowers (tassel) produces 20,000,000 to 50,000,000 grains of pollen. About 45,000 times as many pollen grains are produced as ovules.

FIG. 116. The imperfect flowers of field pumpkin (*Cucurbita pepo*) with perianth removed. *A*, pistillate flower. *B*, staminate flower. (After Robbins, from *Botany of Crop Plants*.)

In pines, the pollen is produced in very large quantities, and veritable showers of pollen may be seen falling from the trees when it is being shed.

It is now well known that pollen is one of the chief causes of hay fever or bronchial asthma. Pollen grains, carried by air currents, reach the membranes of the respiratory tract. If the individual receiving them is "sensitive" to the particular pollen, he develops hay fever. Listed among the worst hay-fever plants are the following: ragweeds, wormwoods, pigweeds, many grasses, including corn, oats, timothy, and such trees as oak, black walnut, cedar, elms, and poplars.

The principal pollinating insects are bees, the most efficient of which are the honeybee and the bumblebee. It is reported that French and sugar prunes in California, and Napoleon and Black Tartarian cherries, produce very light crops of fruit unless a large number of bees are present in the orchard at the time of blooming.

The moths and butterflies are also important pollinating agents. With their long mouth parts they are particularly adapted for securing nectar from flowers with long tube-shaped corollas, such as larkspur, columbine, and nasturtium.

Some plants are normally self-pollinated. This is true of most cereals, except rye and corn, of garden peas, tobacco, cotton, and many other plants. In a great many species, however, cross-pollination is the rule, and their self-pollination may be attended by a

reduction in their vigor and productivity; but there are reasons for believing that the advantages of cross-pollination and disadvantages of self-pollination have been overstated.

Artificial Pollination.—Artificial methods of pollination are practiced by plant breeders in making crosses. The flowers to be cross-pollinated are emasculated (i.e., the anthers are removed before pollen is shed), and then kept

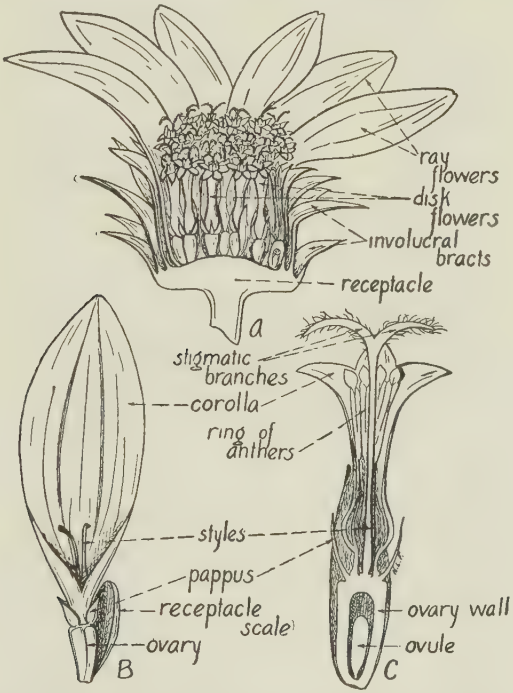


FIG. 117. Jerusalem artichoke (*Helianthus tuberosus*). *A*, longitudinal section of the head (*inflorescence*), showing the numerous separate flowers attached to a common receptacle. *B*, a single ray flower. *C*, a single disc flower, cut lengthwise. (After Robbins, from *Botany of Crop Plants*.)

covered with a bag until the pistils are pollinated and the stigmas have passed the receptive stage.

Greenhouse tomatoes do not set fruit well unless artificially pollinated. This may be accomplished by jarring the plants when the anthers are shedding pollen, or by the collection of pollen on a spoon or glass slide or small brush and removing it to other flowers.

In the date palm, staminate and pistillate flowers are borne on different individual trees. Consequently, it is necessary in a date grove that there be a number of staminate trees scattered among the pistillate ones to insure pollina-

tion. Or a good crop of dates may be secured by cutting off the inflorescence of a staminate tree and tying it into a pistillate tree near the clusters of pistillate flowers, or by collecting large quantities of pollen and dusting the pistillate flowers when the stigmas are receptive.

FIG. 118. Flower heads of Shasta Daisy (*Chrysanthemum leucanthemum*) and, on the left, ray flowers somewhat enlarged. Above, the familiar type with strap-shaped ray flowers, showing, in the enlarged flower, the tips of three of the five petals which together form the (strap) corolla of the ray flower. Below, a variety with tubular corolla-like ray flowers. The ray flowers of most members of the sunflower family (the Compositae) are generally incomplete, the stamens being absent.

It is necessary in growing Smyrna figs to resort to artificial pollination, technically known as "caprification." A wild fig, the caprifig, although of no commercial importance in the production of edible fruit, is indispensable to the Smyrna fig grower. When caprifig fruits are mature, their issues from them a wasp, known as the fig wasp. As the wasps emerge they become covered

with pollen. In search of a place to lay their eggs, they go to the partly mature figs of Smyrna. They enter the orifice of the fig, scatter pollen on the stigmas, and fertilization of the ovules follows. In Smyrna fig culture the mature fruits of caprifigs, harboring fig wasps, are usually placed in small baskets or open bags and fastened in the Smyrna trees.

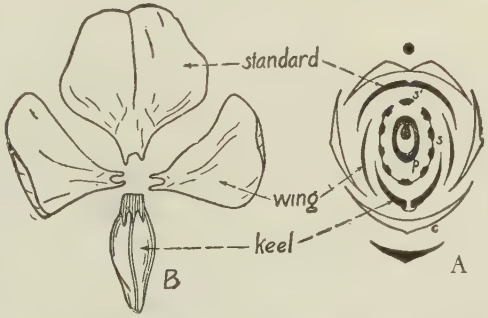


FIG. 119. Bilaterally symmetrical flower of a legume (*Leguminosae*). *A*, floral diagram of horse bean (*Vicia faba*). *B*, corolla of a sweet pea flower (*Lathyrus odoratus*), dissected, diagrammatic. (*A*, after Eichler, *B*, after Bergen, from Robbins' *Botany of Crop Plants*.)

Self-Sterility. — Many of the commercial varieties of apples, pears, plums, and other fruits are self-sterile. That is, they are unable to develop seed or set a crop of fruit when pollinated with their own pollen. For example, in certain sections of the country the Spitzenburg apple is self-sterile but capable of being fertilized with pollen from a number of other varieties, such as Yellow Newton, Jonathan, and Baldwin. Obviously, it would not be well to plant solid blocks of Spitzenburg. It should be alternated with rows of some one of the other varieties, the pollen of which is capable of fertilizing it. Judicious interplanting of varieties becomes good orchard practice. If an orchard of one variety proves to be unfruitful because it is planted in a solid block, it is possible

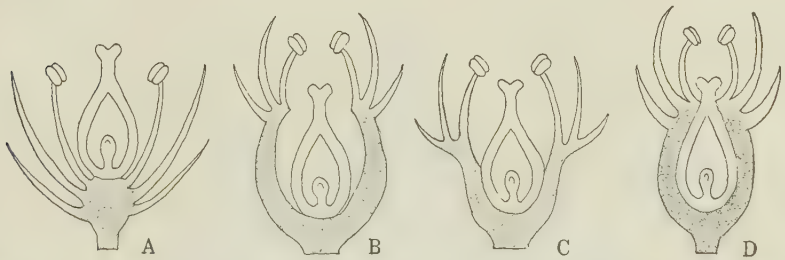


FIG. 120. Diagrams showing the structure of (*A*) hypogynous flower, (*B* and *C*) perigynous flower, the latter being of a type in which the lower portion of the ovary is buried in the receptacle, and (*D*) epigynous flower.

to remedy the situation by grafting into some of the trees shoots of a variety which will furnish suitable pollen. This self-incompatibility or self-sterility, is apparently due to the failure of the pollen to grow down the style and bring about fertilization.

Germination of the Pollen Grain.—The mature pollen grain at the time it is discharged from the anther is a spherical or oval

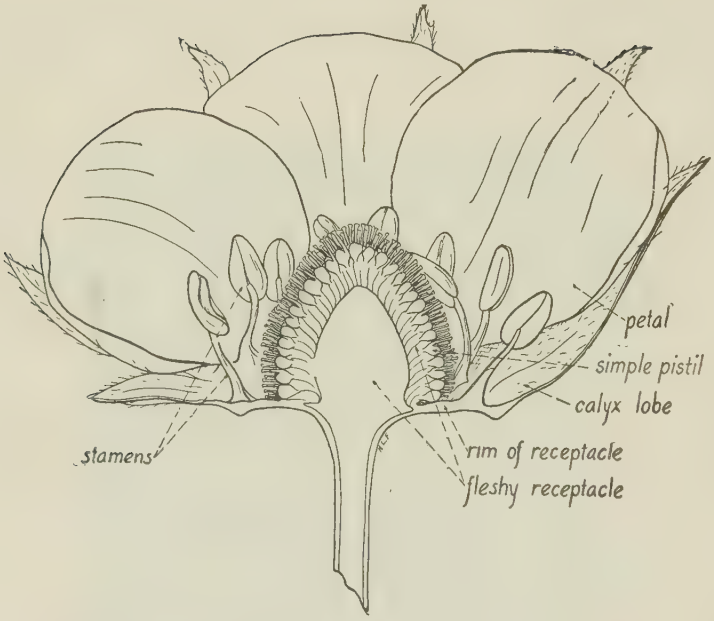


FIG. 121. Median longitudinal section of the flower of strawberry (*Fragaria*) showing the numerous separate carpels attached to a common receptacle. (After Robbins, from *Botany of Crop Plants.*)

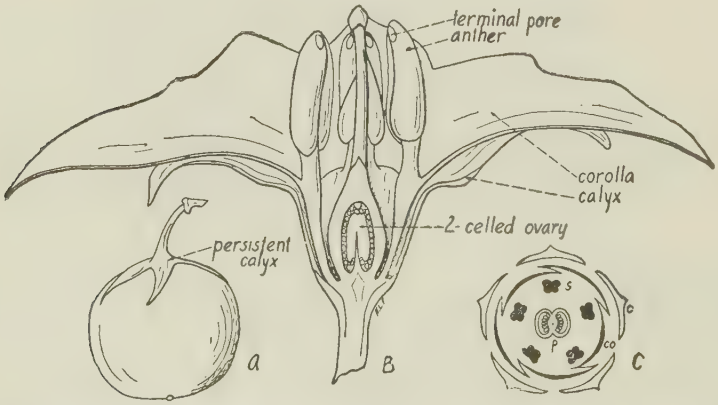


FIG. 122. Flower and fruit of potato (*Solanum tuberosum*). *A*, mature fruit, a berry. *B*, median lengthwise section of the flower. *C*, floral diagram. Note that the stamens are attached to the sympetalous corolla. (After Robbins, from *Botany of Crop Plants.*)

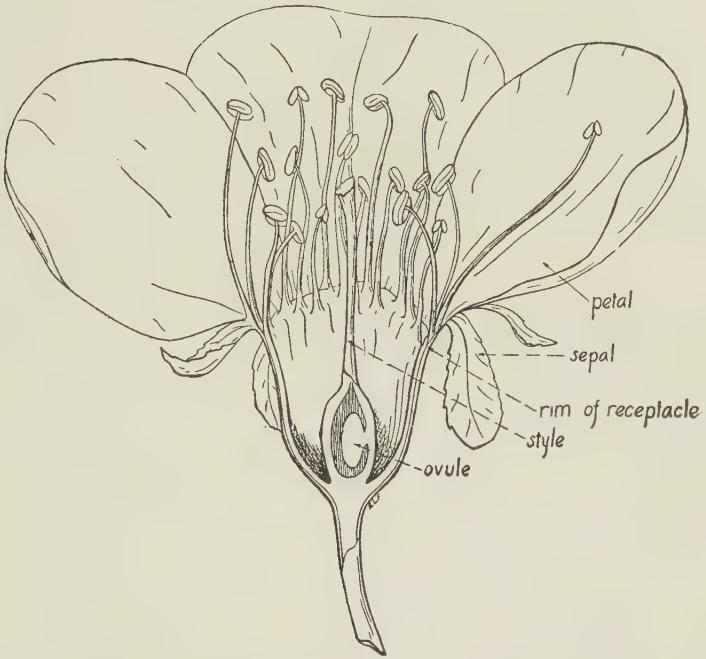


FIG. 123. Perigynous flower of sour cherry (*Prunus cerasus*) in median lengthwise section. (After Robbins, from *Botany of Crop Plants*.)

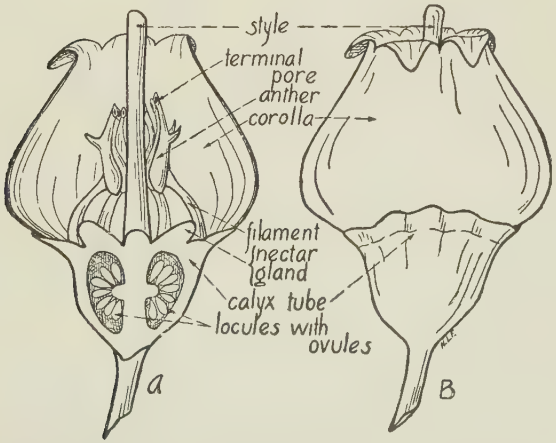


FIG. 124. The epigynous flower of the huckleberry (*Vaccinium*), showing united sepals (*synsepaly*), united petals (*sympetaly*), and united carpels (*syncarpy*). *A*, median lengthwise section. *B*, external view. (After Robbins, from *Botany of Crop Plants*.)

cell with two surrounding walls or membranes. About the time the pollen grain is shed, the single nucleus divides into two, the **generative nucleus** and the **tube nucleus**. These are not separated by a cell wall, but the cytoplasm surrounding the generative nucleus is generally distinctly differentiated from the rest of the cytoplasm of the pollen grain. The pollen grain germinates on the surface of the stigma. By this is meant that it sends out a slender thread-like growth, the **pollen tube**. The protoplasm of the grain absorbs water and swells, breaking the outer wall. The inner membrane is stretched and extends through the break in the outer wall as the limiting membrane of a protoplasm-lined tube. This pollen tube penetrates the tissue of the stigma, grows down through the style, and enters the ovary. The styles of some flowers are hollow, but this is not generally the case, and so the passage of the tube necessitates the secretion of tissue-dissolving enzymes by the advancing tip of the tube. During the growth of the pollen tube the generative nucleus undergoes division, forming two nuclei, the so-called **sperm nuclei** or **male nuclei**. The two male nuclei and the tube nucleus, together with most of the cytoplasm, pass to the tip of the tube and remain at the tip as the tube advances.

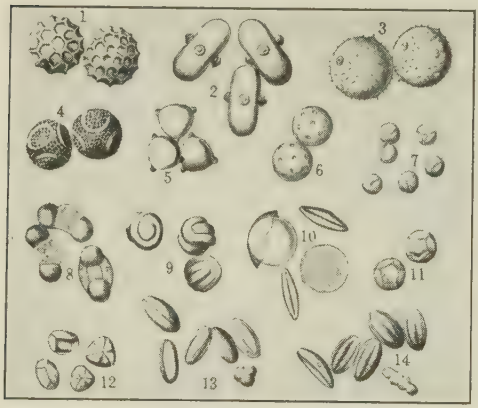


FIG. 125. Pollen grains of various forms and markings. (After Kerner.)

Growth of pollen tubes may be very rapid. Under favorable conditions the pollen tube of corn may grow six inches in twenty-four hours.

Recent experiments indicate that in the case of several species one part of the growth substance, 3-indoleacetic acid, in one million parts of culture solution stimulates the germination of the pollen grains and the growth of the pollen tube.

Fertilization.—We have seen that the mature ovule consists of a stalk, and a central mass of tissue, called the **nucellus**, surrounded

by one or two protective layers of cells, the **integuments.** The integuments completely surround the nucellus except for a pore which leads from the surface of the ovule between the edges of the integuments down to the surface of the nucellus. This pore is called the **micropyle.** Buried in the tissue of the nucellus, in a mature and fully developed ovule, is the **embryo sac.** The mature embryo sac consists of a mass of vacuolated cytoplasm with eight nuclei lying free in it. The two nuclei at the micropylar end of the embryo sac

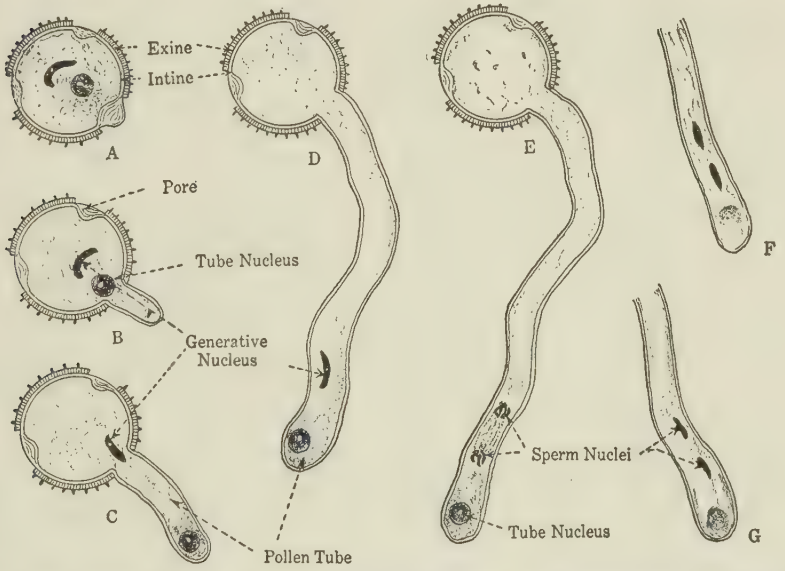


FIG. 126. Stages in the germination of the pollen grain, and development of the pollen tube. Diagrammatic. (Redrawn from Bonnier and Sablon.)

are the so-called **synergids**; near them is the **egg nucleus.** At the opposite extremity of the embryo sac are also three nuclei, termed the **antipodal nuclei.** Between the egg nucleus and the antipodal nuclei are two nuclei which lie close together or in actual contact. These are the **polar nuclei.**

When the pollen tube reaches the ovary it grows toward one of the ovules and enters the embryo sac, generally, through the micropyle and nucellus. After entering the embryo sac, the wall at the tip of the pollen tube breaks and the three nuclei (two sperm nuclei and the tube nucleus), along with some cytoplasm, are dis-

charged into the sac. One of the sperm nuclei moves toward the egg nucleus and fuses with it. This is fertilization. A cell wall is soon formed around this fusion nucleus or fertilized egg nucleus and some cytoplasm. The cell thus formed is called the **zygote**. The second male nucleus passes to the center of the sac, where it unites with the polar nuclei, or, in case these have previously combined, with the single resultant nucleus. The nucleus thus produced by the fusion

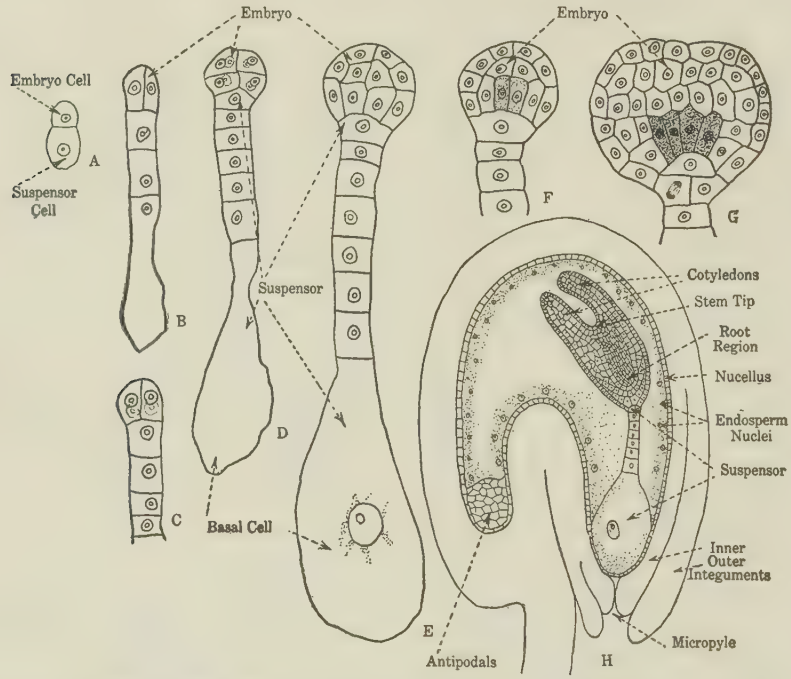


FIG. 127. Stages in the development of the embryo of shepherd's purse (*Capsella*) a dicotyledonous plant. (*A-G*, redrawn from Coulter and Chamberlain); (*H*, redrawn from Bergen and Caldwell.)

of the three nuclei is called the **endosperm nucleus**. The fusion of these three nuclei is sometimes called **double fertilization**.

Only one pollen tube functions in the fertilization of each embryo sac. Many more pollen tubes may grow down the style than there are ovules in the ovary, in which case many tubes do not function.

In wheat, fertilization usually occurs between one and two days after pollination. This interval represents the time necessary

for the pollen grain to germinate, and for the pollen tube to grow down through the style to the embryo sac in the developing ovule. This time varies widely in different species and with different environmental conditions, particularly temperature.

Formation of the Embryo.—By a series of cell divisions the zygote ultimately forms the rudimentary plant or embryo of the seed, further development of which during germination of the seed produces the mature plant. Figure 127 shows a number of stages in the development of the embryo from the zygote.

Formation of the Endosperm.—Shortly after fertilization, the endosperm nucleus undergoes repeated divisions which are not attended by the immediate formation of cell walls. The cytoplasm of the embryo sac meanwhile increases in amount as food is supplied from the surrounding tissue of the ovule. The numerous endosperm nuclei and this cytoplasm soon line the embryo sac and finally may increase until they fill the entire space around the embryo. Sooner or later there is an almost simultaneous formation of cell walls between all the endosperm nuclei, resulting in a mass of tissue called the **endosperm**, which serves as a source of food for the developing embryo.

Development of the Seed.—Fertilization stimulates the tissues outside the embryo sac to active growth so that the whole ovule increases greatly in size. Thus the seed may grow to be hundreds of times as large as the unfertilized ovule. In addition to increasing in number, the cells of one or both integuments of the ovule undergo great changes in the nature and thickness of their cell walls, and thus the **seed coats** are formed. The nucellus in most cases does not take any part in the development of the seed after fertilization but practically disappears through compression or absorption of its cells before the seed is fully developed. The endosperm grows actively for a longer or shorter period of time, depending on the species. Similarly, the length of time it remains after completing its development varies. In some plants, such as the bean (*Phaseolus*), pea (*Pisum*), and other legumes, the endosperm is entirely used up by the embryo before the seed ripens. In such cases the mature seed consists only of an embryo and one or more seed coats. In other species (all grasses, for example) much of the endosperm remains

even in the ripe seed. It is then available as a source of food for the embryo during germination.

Effect of Fertilization on Fruit Formation.—The effect of fertilization generally extends to the ovary and starts growth and differentiation of its cells, resulting in fruit formation. In the apple, pear, and several related plants, the receptacle is also stimulated to growth and takes part in the formation of the fruit. There are, however, many plants in which the stimulation of fertilization is not essential to fruit production.

CHAPTER VIII

FRUIT AND SEED

THE FRUIT

Fruits, including the seeds they contain, constitute the most important source of man's food supply. Although the stem of the sugar cane and the root of the sugar beet furnish most of the sugar we use, and although the tuber of the Irish potato and the roots of the sweet potato, turnip, and carrot are important elements in our diet, there can be no doubt that fruits and seeds are, of all plant parts, the most important as food sources.

Our present-day fruits, in all their variety, adapted as they are to many different soils and climates and suited to the tastes of many people, have been derived from wild plants which in their primitive state yielded edible fruits of inferior quality.

In the botanical sense, a fruit is a matured ovary of a flower, including its one or more seeds and any part of the flower which remains closely associated with the ovary. This definition would include such one-seeded, dry fruits as corn, oats, wheat, and other cereals, which are commonly spoken of as "seeds," as well as tomatoes, the pods of beans and peas, walnuts, acorns, and many other structures which are not fruits in the popular sense.

The Development of the Fruit.—The immediate result of fertilization is the initiation of a series of changes in the embryo sac and ovule, which lead to the development of the seed. Thus, the stimulus of fertilization, the nature of which is not well understood, extends its influence not only to the ovule, but to the ovary as well, and in some cases beyond the ovary to include tissue of other flower parts. In the great majority of plants, fruit does not form unless pollination is followed by fertilization and this by normal seed development.

In most fruits there is rather close correlation between the number of seeds formed and the size, form, and even the composition

of the fruit. For example, in grapes, there is a close relation between the number of seeds and the weight of the flesh, those grapes which have the greatest number of seeds generally being the largest. It is a common observation that, as in the case of the tomato, locules which do not contain a number of good seeds are not well developed, and fruits with such locules are irregular and distorted in form.

Fruit development sometimes takes place without seed formation and without the processes (pollination and fertilization) which must normally precede seed development. Such development is spoken of as **parthenocarpy**; the fruits are practically always seedless. Very rarely, however, seeds may develop parthenogenetically (without fertilization) in parthenocarpic fruits. Moreover, not all seedless fruits are parthenocarpic, for seedlessness may be due to abortion of the embryos after fertilization rather than to absence of fertilization.

A number of our cultivated plants regularly bear parthenocarpic fruits which are seedless. Familiar examples are seedless raisin grapes, bananas, and pineapples.

Parthenocarpic fruits have been artificially produced by treating the pistil of a flower in the bud stage with various growth-promoting substances (auxins). In this connection it is of interest to note that the ovaries of flowers in these varieties which normally produce parthenocarpic fruits (such as grapes, lemons, and oranges) have a higher auxin content than the ovaries of varieties which do not normally develop fruits parthenocarpically.

Structurally, the ovary walls are relatively simple, being largely made up of parenchyma cells; but the structure of the fruit wall or **pericarp** into which the ovary wall develops is sometimes quite complex, often three distinct layers being present. The outermost layer, the **exocarp**, usually consists of a single layer of cells, the epidermis. The **mesocarp** (middle layer) is a very thin layer in some fruits, and as much as several centimeters thick in others. The **endocarp** (inner layer) may consist of a single layer of cells or a number of cell layers (modified in one of a number of different ways).

In the natural ripening of fruits, certain chemical changes occur. For example, there is usually a progressive increase in the percentage of dry matter, in total sugars, in soluble solids, etc. Efforts have been made to hasten the ripening of fruits by artificial means. Artificial ripening has appeared commercially desir-

able in such fruits as citrus, banana, date, tomato, cantaloupe, pineapple, and persimmon. Among the various methods employed, the exposure of the unripe fruit to ethylene gas has been most widely and successfully used.

TYPES OF FRUIT

According to the number of ovaries involved in their formation, fruits are classified as **simple**, **aggregate**, and **multiple**.

FIG. 128. Fruits of common plants, illustrating, with the exception of *E* and *F*, the principal methods of dehiscence. *A*, pod of pea (*Pisum sativum*). *B*, silique of mustard (*Brassica*). *C*, capsule of Jimson weed (*Datura*), septicidal dehiscence. *D*, three follicles of larkspur (*Delphinium*). *E*, samara of maple (*Acer*). *F*, aggregate fruit of raspberry (*Rubus*). *G*, capsule of violet (*Viola*), loculicidal dehiscence. *H*, capsule of poppy (*Papaver*), poricidal dehiscence.

A simple fruit consists of a single enlarged ovary. The fruits of the great majority of flowering plants belong to this class. They may have the pericarp fleshy and so be known as **fleshy** fruits; or they may have the pericarp dry, and be known as **dry** fruits.

The principal types of simple, fleshy fruits are the **berry**, **drupe**, and **pome**. In the **berry** the ovary wall is fleshy and encloses one or more seeds. Examples: grape, gooseberry, pepper, tomato, date,

and some hard fruits or fruits with leathery rind such as squash, cucumber, orange, and lemon. The drupe, or stone fruit has a characteristic hard and stony endocarp enclosing the seed; outside the endocarp is the juicy and usually edible mesocarp, which is covered by a thin "skin" or exocarp. Examples: cherry, peach, almond,

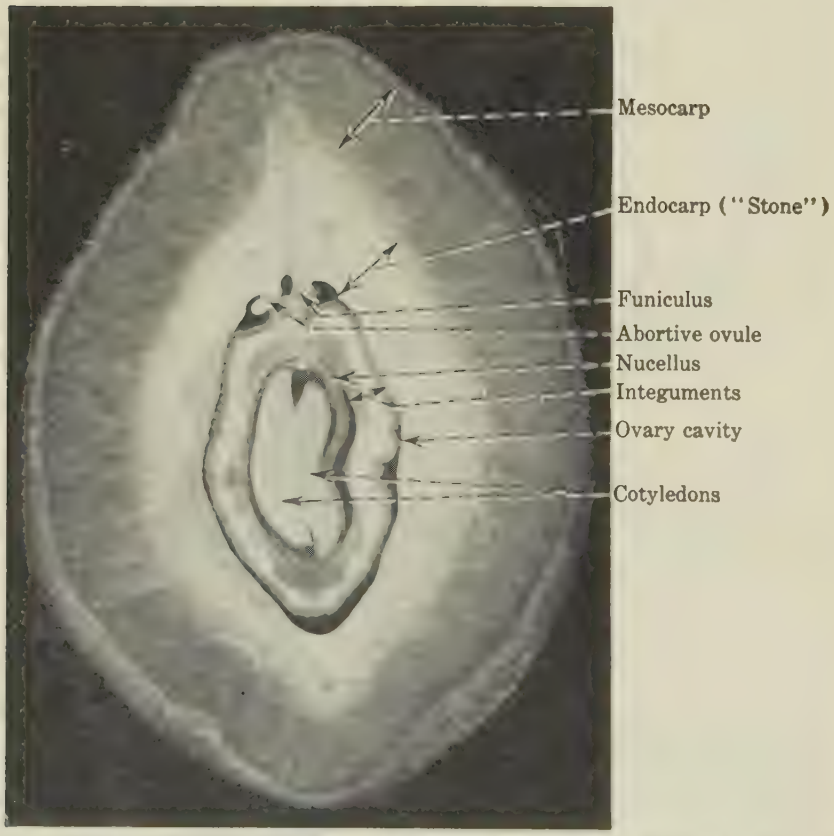


FIG. 129. Median lengthwise section of immature almond fruit (drupe). Note the large fertile ovule, and the small abortive ovule. Vascular bundles of the pericarp are clearly seen.

plum, and olive. The pome consists chiefly of fleshy receptacle which has grown up about the outer portion of the pericarp, which is also fleshy, and surrounds an inner papery portion, known as the "core." Examples: pear, apple, and quince.

The dry fruits are classified into those which open when ripe—

the **dehiscent** fruits, and those which do not open when ripe—the **indehiscent** fruits. Examples of plants having dehiscent fruits are:

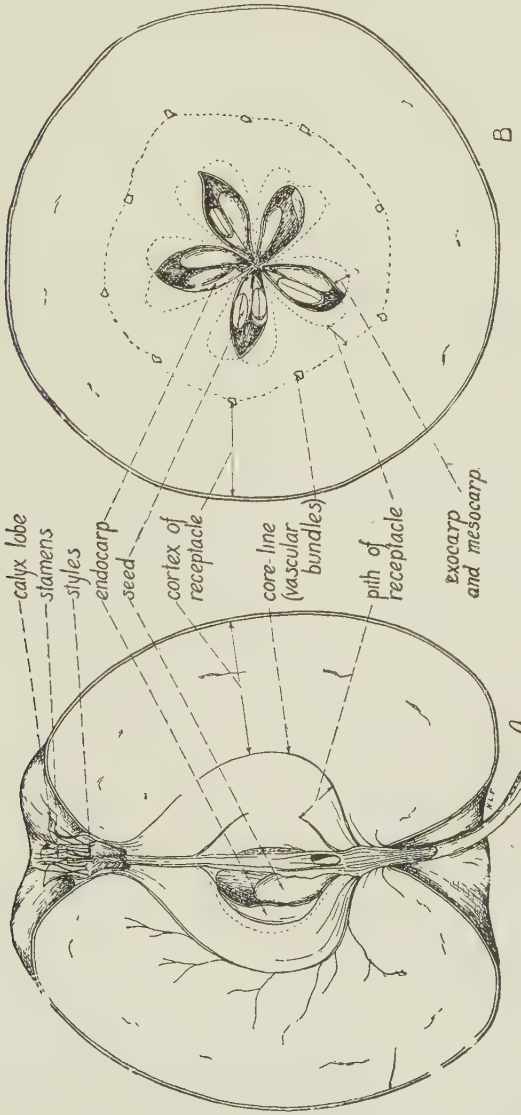


FIG. 130. The mature apple fruit (pome). *A*, median longitudinal section. *B*, cross section. (After Robbins, from *Botany of Crop Plants.*)

the poppy, lily, milkweed, pea, and bean. The fruits of sunflower, wheat and other cereals, maple, and hazelnut are examples of indehiscent fruits.

An aggregate fruit is one composed of a single receptacle upon which are massed many similar true fruits; it is derived from a single flower having many pistils. The strawberry, raspberry, and blackberry are aggregate fruits.

Whereas an aggregate fruit is derived from a single flower having many pistils, a multiple fruit is developed from the ovaries of many separate and yet closely clustered flowers. Among the most familiar examples of plants bearing multiple fruits are the mulberry, pineapple, and fig.

THE SEED

Seeds are of great economic importance, not only because they are food-storage organs but also because man uses seeds as a means of multiplying useful plants. In our ordinary agricultural operations, the seed is usually the beginning of the crop. Seeds also furnish man with a large proportion of his food and with many important products used in the industries. A large part of the world's supply of flour is made from wheat. Rice is a food for more human beings than is any other grain. It is the principal food of the densely populated regions of China, India, and the neighboring islands. No other cereal is put to such a variety of uses as is corn. Corn oil is obtained from the embryo, and about 50,000,000 bushels of corn are used annually in the United States in the manufacture of commercial starch. Glucose and artificial gums are made from corn starch. Of the many products used in the industries which are also secured from seeds, perhaps the most important are the various oils and fats produced from the seeds of such plants as the coconut, cotton, flax, soy bean, castor-oil plant, and peanut. These oils are used in the manufacture of soap and substitutes for butter and lard, and as salad oil. Linseed oil is used in making paints, varnishes, artificial leather, oilcloth, and linoleum. The vegetable ivory of commerce, from which great numbers of buttons are made, is secured from the seed of the South American palm (*Phytelephas*). Many

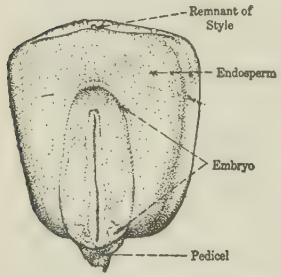


FIG. 131. One-seeded, indehiscent fruit (grain) of corn (*Zea mays*), external view. The small projection at the upper end of the grain is the base of the style (strand of corn silk).

other kinds of seeds furnishing important commercial products might be mentioned.

Within recent years the soybean (*Soja max*) has become a very prominent economic plant. Manchuria leads in production, followed in order by Korea, Japan, Dutch East Indies, and the United States. Food and industrial uses for the soybean, the oil and meal, have developed with startling rapidity. The

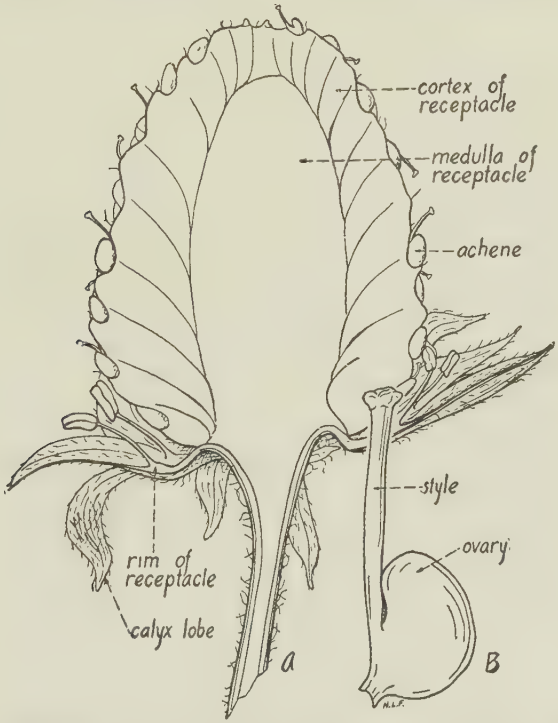


FIG. 132. The aggregate "fruit" of strawberry (*Fragaria*). *A*, the "fruit" in median lengthwise section; *B*, single achene. (After Robbins, from *Botany of Crop Plants*.)

soybean now is used in the manufacture of such products as paints, enamels, varnish, glue, printing ink, linoleum, plastics, adhesive and sizing materials, shortenings, foundry cores, livestock feeds, flour (soya flour), soy sauce, dietetic foods, and beverages. The principal constituents of the seeds which have commercial value are oil (about 18 per cent), protein (about 40 per cent), and certain non-nitrogenous extractives (about 28 per cent), chief of which are phosphatids. Soybean protein is the basis of innumerable plastics. Soybean plastics enter into the construction of distributor parts for certain makes of automobiles, gear shift lever knobs, light switches, horn buttons, coil parts, and window frames; and all sorts of articles for the home and office.

The epidermal hairs of cotton seed furnish the cotton of commerce. Cotton fibers are rich in cellulose. As a rule, there are two kinds of hairs on the cotton seed: (a) long hairs, the lint or "staple" and (b), short hairs or "fuzz." The long hairs vary in length from 0.9 inch in American upland types of cotton to

FIG. 153. Acorns (nut) of white oak (*Quercus alba*). (Photograph furnished by L. W. Brownell.)

1.6 inches in Sea Island types. The quality of fiber depends chiefly upon the number and regularity of twists in it, and upon its length and fineness.

THE DEVELOPMENT OF THE SEED

We learned, in the last chapter, of the origin of the seed in the ovary of the flower and of the development of the ovule after fertilization into a seed. The following outline shows the rôle played by

each of the flower parts and organs as the flower develops into the fruit with its seeds:

FLOWER		IN THE MATURE FRUIT
Calyx		Adherent or deciduous
Corolla		Usually deciduous
Stamens		Usually deciduous
Pistil	Stigma	Withers; remnant may be present
	Style	Withers; remnant may be present
	Ovary wall	Pericarp: Exocarp, Mesocarp, Endocarp
	Placenta	Variously modified
		IN THE SEED
	Ovule (seed): Funiculus	Seed stalk
	Ovule (seed): Raphe	Raphe
	Ovule (seed): Chalaza	Chalaza
	Ovule (seed): Micropyle	Micropyle
	Ovule (seed): Nucellus	Perisperm (seldom present) or a thin layer of compressed cells
	Embryo sac: Egg nucleus (fertilized)	Embryo
	Embryo sac: Polar nuclei (fertilized)	Endosperm

THE STRUCTURE OF THE SEED

Seeds vary a great deal in shape, size, color, surface markings, internal structure, and amount and nature of stored food, but most seeds consist of the following parts:

Seed coat or coats.
Remains of nucellus.
Endosperm—sometimes lacking.
Embryo
- Plumule.
- Cotyledons (sometimes only one).
- Hypocotyl.
- Radicle.

A description of the common bean will serve to call attention to some features of structure common to many seeds. A large oval

scar called the hilum, near the middle of one edge of the seed, marks the place where the seed broke from the stalk or funiculus in the fruit (pod). At the end of the hilum is a small opening, the micro-

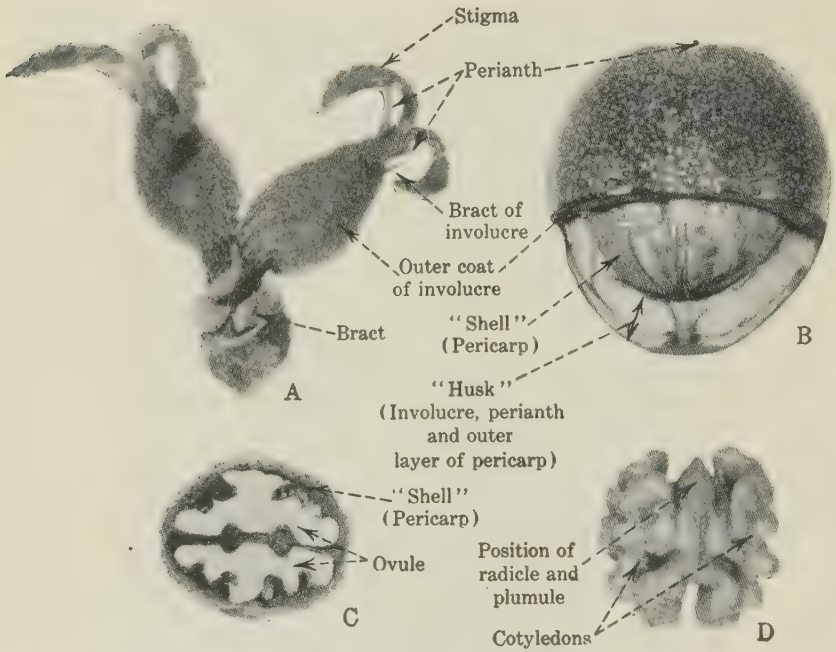


FIG. 134. Flowers and fruit of English walnut (*Juglans regia*). *A*, two pistillate flowers at time of fertilization; *B*, mature fruit; *C*, cross-section of "nut" with "husk" removed; *D*, single ovule, consisting of a large, irregularly shaped ovule ("meat"), covered with brown papery seed coat, with two divided cotyledons, a radicle and plumule. (Photographs furnished by Nast.)

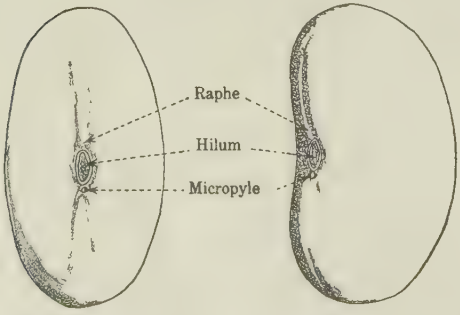


FIG. 135. The seed of a common bean (*Phaseolus vulgaris*) showing two external views.

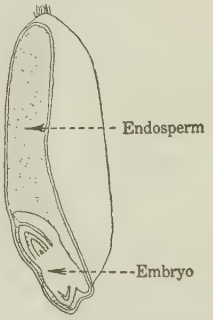


FIG. 136. The fruit (grain) of wheat (*Triticum*) in longitudinal section.

pyle, which was present in the ovule at the time of fertilization. The micropyle is more easily seen if the seed is soaked in water. The position of the radicle is indicated by an elevation of that part of the seed coat which is adjacent to the micropyle. When the seed is soaked in water and the seed coat removed, the embryo is visible. This embryo consists of the following parts: (1) two cotyledons or

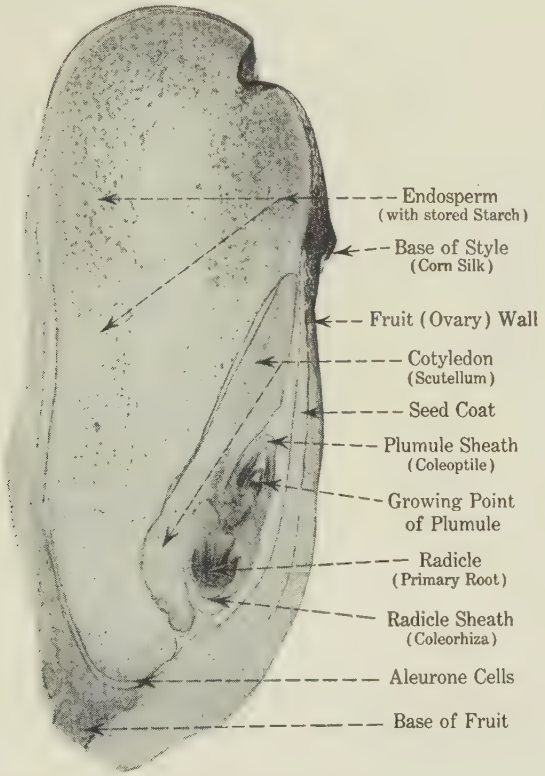


FIG. 137. Photomicrograph of a lengthwise section of a grain of corn (*Zea mays*).

seed leaves, between which is (2) the plumule with two minute foliage leaves, enclosing the growing point, and (3) the hypocotyl terminating in (4) the rudimentary root or radicle. The two cotyledons are large and fleshy and contain stored food, chiefly starch.

The endosperm is lacking in the mature bean seed, having been absorbed by the developing embryo. In seeds of this type the reserve food is stored in the cotyledons.

Conspicuous examples of seeds with endosperm are castor-oil seed, corn, wheat, and other cereals. In the castor-oil seed, the embryo consists of two flat cotyledons, a very short hypocotyl, a diminutive plumule, and a short radicle. The embryo is embedded in a massive endosperm. In wheat, as in all members of the grass family, the embryo has but one cotyledon. It is a structure which lies in contact with the endosperm and is specialized to absorb food from the endosperm and turn it over to the growing parts of the

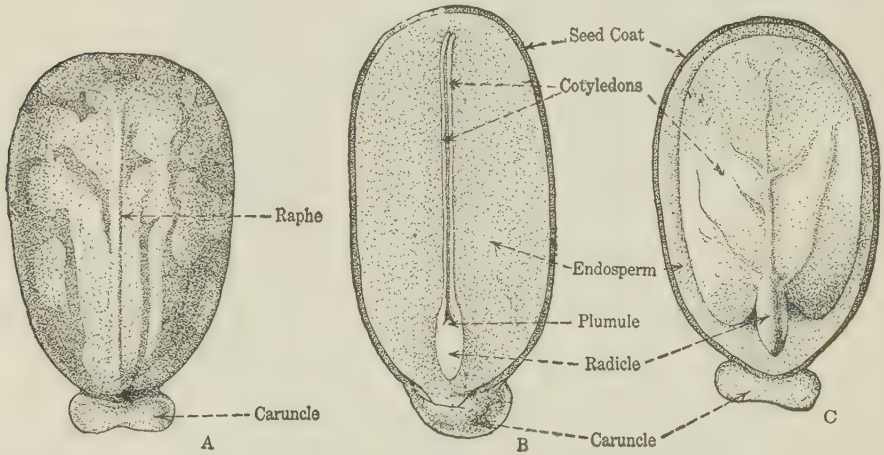


FIG. 138. The seed of castor-oil plant (*Ricinus communis*). *A*, external view. *B*, median longitudinal section cut at right angles to the broad surface of the cotyledons. *C*, median longitudinal section, cut parallel with the broad surface of the cotyledons.

embryo; accordingly, the cotyledon remains within the seed during germination.

KINDS OF FOOD STORED IN SEEDS

The principal kinds of food stored in seeds are as follows:

1. Carbohydrates, chiefly:
   - (*a*) Starch.
   - (*b*) Hemi-celluloses.
   - (*c*) Sugars.
2. Fats.
3. Proteins.

Starch.—This is the commonest form of food stored in seeds. It may occur either in the embryo or in the endosperm. It is formed by the leucoplasts in the cells of the developing seed from the sugar

which is conducted to the seeds from other parts of the plant. The form of the starch grains produced by the leucoplasts varies in different plants, and the characteristic forms and markings of the grains are valuable aids in the recognition of certain adulterations in foods.

Hemi-celluloses.—The hemi-celluloses are complex reserve carbohydrates. They constitute the greater part of the thickened cell

FIG. 139. Starch grains from different sources. 1, *Diffenbachia* (After Meyer); 2, *Triticum sativum*; 3, *Phaseolus lunatus*; 4, *Phaius*; 5, *Canna*; 6, *Solanum tuberosum*; 7, *Zea mays*. (2-7, after Reichert.)

walls of the endosperm in the seeds of such plants as the date (*Phoenix dactylifera*), onion (*Allium*), coffee (*Coffea*), and vegetable ivory palm (*Phytelephas monocarpa*). The hard endosperm of the last-named plant is used commercially for the manufacture of buttons, umbrella handles, and other objects. Hemi-celluloses are quite different from true cellulose, and, since they are more easily rendered soluble (digested), are more available as reserve food for the developing embryo at germination.

Sugars.—Although starch is the carbohydrate found most commonly and in largest quantity in seeds, soluble carbohydrates

(sugars) are frequently present. Generally the sugar stored in seeds is cane sugar (sucrose); as much as 11 per cent of this sugar is present in the seeds of sweet corn and chestnut. Cane sugar is also present in almonds, pistachios, and other nuts. Certain varieties of peas are so rich in sugar that they have a very sweet flavor.

Fats.—Fats are of general occurrence in both vegetative and reproductive organs of plants, but are much more abundant in seeds than elsewhere, and constitute an important reserve food. Fats occur in the form of globules within the protoplasts of the cells, usually being much more abundant in the embryo than in the endosperm.

Proteins.—The proteins are organic compounds containing oxygen, hydrogen, carbon, nitrogen, generally sulphur, and often phosphorus. Next to water, proteins are the most abundant constituents of protoplasm, and they are essential for the production of new protoplasm. Stored proteins are found in all seeds, occurring very abundantly in seeds of members of the bean family (Leguminosae.)

DISSEMINATION OF SEEDS AND FRUITS

The migration of plants over the surface of the earth is accomplished in many different ways. We have seen that some plants migrate by means of runners, or rhizomes; this method is very slow. The most effective and rapid plant migration is by means of seeds or fruits.

There are many structural modifications by which dissemination of seeds and fruits is secured. **Wind, water, and animals, including man,** are the chief agencies in seed and fruit dissemination. Fruits and seeds which are winged (example, maple) or have long silky hairs (cotton, milkweed) or tufts of hairs (dandelion) are readily carried by wind. Some fruits have membranous envelopes containing air and are carried easily by wind or water. Many seeds will float, though lacking special adaptations which insure buoyancy. Numerous fruits and seeds have hooks, barbs, beards, and spines which adhere to the hair of animals or to the clothing of man. The seeds of fleshy edible fruits are scattered by birds and animals, and nuts are carried away and hidden by squirrels. Man, in his various agricultural operations, is responsible for the spread of weed seeds.

Probably the most common and effective means of introducing and disseminating weeds is by the sale and distribution of impure commercial seeds.

FIG. 140. Various seeds and fruits showing devices for dissemination. *A*, winged fruit of maple (*Acer*). *B*, winged fruit of ash (*Fraxinus*). *C*, winged fruit of elm (*Ulmus*). *D*, winged seed of pine (*Pinus*). *E*, barbed fruit of Spanish needles (*Bidens*). *F*, milkweed (*Asclepias*) seed with tuft of hair. *G*, hairy seed of cottonwood (*Populus*). *H*, fruit of dandelion (*Taraxacum*) with parachute-like tuft of hairs. *I*, hooked fruit of cockle-bur (*Xanthium*). *J*, fruit of *Clematis* with long plume-like style. *K*, fruit of ground cherry (*Physalis*), with membranous envelope. *L*, bearded fruit of porcupine grass (*Stipa*).

Weed seeds are carried in screenings, baled hay, the packing about trees, and in feed stuffs. Some seeds are uninjured in passing through the digestive tracts of animals and consequently are spread on the field in manure. The use of feeding stuffs containing live seeds may result in the spread of noxious weeds.

A threshing machine may carry weed seeds from farm to farm. In the irrigated sections water is one of the chief means of spreading seeds; ditch banks are densely overgrown with weeds which shed their seeds in the water; the seeds are carried down stream, given a good soaking in transit, and planted on a well-watered soil—all conditions being ideal for germination.

In certain western states there is a weed known as "puncture vine" (*Tribulus terrestris*), introduced from the Mediterranean region. Its introduction into western United States was by the importation of livestock, especially sheep. The plant bears a fruit consisting of a cluster of five spiny nutlets or burs. The nutlets, which fall apart at maturity, are readily disseminated by animals or rubber-tired vehicles because one of the spines usually points upward however the bur lies on the ground. The fact is that the automobile has given the puncture vine a very easy and rapid means of dissemination. Also, it is known that in certain instances the airplane has carried the burs in its tires from one landing place to another.

Fig. 141. The squirting cucumber, *Ecballium elaterium,* one of a number of different kinds of "explosive" fruits in which seed dissemination results from violent rupture of the fruit. (From Bocquillon.)

In the case of certain species, such as the tumbleweeds (Russian thistle, witchgrass, tumbling pigweed, and others), the whole plant is carried by the wind, rolling for many miles over treeless areas, scattering seed as it travels. Russian thistle is a splendid example of a plant which has spread with alarming rapidity in the United States. It was introduced here in 1886 in flax seed brought from Russia and sown near Scotland, South Dakota. By 1895 it had spread to sixteen states and thirteen Canadian provinces. Today it infests hundreds of thousands of acres of agricultural lands from the Mississippi Valley to the Pacific Coast.

THE GERMINATION OF SEED

A seed is essentially a young plant (embryo) arrested in its development. An individual plant does not start its life as a seed. It will be recalled that, instead, it begins as a single cell called a zygote. The new individual plant comes into existence at the time of fertilization—when a sperm (male) nucleus from the pollen tube

fuses with the egg (female) cell in the embryo sac of the ovule, forming a zygote. This single protoplast produced by the fusion of two protoplasts undergoes repeated division, and by growth and differentiation there results a young plant which, with its surrounding protecting coats and its stored food, is called the seed. After the seed has matured there is normally a period during which growth and development of the embryo are at a standstill. Resumption of these activities is called germination.

Conditions Necessary for Germination.—For this resumption of growth and development the following external conditions are essential: (1) a sufficient supply of water, (2) a favorable temperature, and (3) a supply of oxygen. If any one of these is lacking the seed will not germinate.

The seeds of a few species, including mistletoe (*Viscum album*) and the strangling fig (*Ficus aurea*), fail to germinate unless exposed to light.

Water.—Water plays a most important rôle in the germination of seeds.

1. Water softens the seed coats, and thus enables the embryo to break through them more easily.

2. The water absorbed by embryo and endosperm causes the seed to swell, and this results in the bursting of the seed coats.

3. Water facilitates the entrance of oxygen into the seed. Dry cell walls are almost impermeable to gases; but if the walls have imbibed considerable water, gases can diffuse quite readily through them. As the walls of the cells of the seed coats and embryo take up water, an increased oxygen supply to the living cells results and more active respiration is made possible. On the same account, the carbon dioxide produced by respiration is able to diffuse outward.

4. Water dilutes the protoplasm and permits its various normal functions, including digestion, respiration, and assimilation, to go on actively. Since the protoplasm of the cells of the embryo and other living parts of the seed loses most of its water before the seeds are shed, its activities are almost completely suspended from that time until germination.

5. Water makes possible the transfer of soluble food from the endosperm or cotyledons to the growing points of the embryo, where food is necessary for the building up of new protoplasm.

Favorable Temperature.—For the seeds of any kind of plant there is a temperature, called the **minimum temperature,** below which germination will not take place. There is also a **maximum temperature** above which the seeds will not germinate, and an **optimum temperature** at which germination goes on most rapidly. These cardinal temperatures vary widely in different species. For example, it is quite well known that cucumbers and melons require a higher temperature for germination than do wheat, barley, and some other small cereals. The seeds of "cool season crops," such as peas, lettuce, radish, and small cereals, will germinate readily at 50° to 60° F., whereas corn, pumpkin, cucumber, eggplant, and other "warm season crops" require a temperature of 70° to 80° F. to give good germination.

Oxygen.—It must be kept in mind that all living cells of the seed must respire in order to maintain life, and that some oxygen is necessary in this process. In the resting stage, the seed requires very small amounts of oxygen, but when germination starts it demands a greater amount. That germinating seeds respire actively is shown by the large quantities of carbon dioxide they give off, and also by the heat liberated in the process. Even though there is sufficient water and warmth, unless seeds are planted so that free oxygen can reach them, they will not germinate. If seeds are planted too deep in a heavy clay soil, or in a soil that is too wet, they are quite likely to have a poor supply of oxygen and to germinate slowly. It is true that some seeds, those of rice, for example, will germinate with a very small amount of oxygen, even with that which is present in water in which they may be submerged. But, if the water is boiled and cooled before the rice seeds are placed in it, and thus most of the oxygen in solution removed, and if the surface of the water is covered with a thin film of oil to prevent the absorption of oxygen by the water, the seeds fail to germinate.

THE PROCESS OF SEED GERMINATION

The principal processes going on in the seed during germination are:

1. Absorption of water by imbibition and osmosis.
2. Digestion.

3. Food transfer.
4. Assimilation.
5. Respiration.
6. Growth.

Water Absorption.—The initial process in seed germination is the absorption of water. The functions of the absorbed water have already been mentioned in connection with the discussion of the conditions necessary for germination.

Digestion.—Most of the carbohydrates, proteins, and fats stored in seeds are in forms that are insoluble in water. Much food in insoluble form is stored elsewhere in plants. These foods in the insoluble form cannot leave the cells in which they are stored or be transferred from cell to cell until they are changed into a form that is soluble in water and hence capable of diffusion. The process of changing insoluble foods or foods which do not diffuse readily, into soluble and easily diffusible forms is called **digestion.** In this process certain substances called **enzymes** are important.

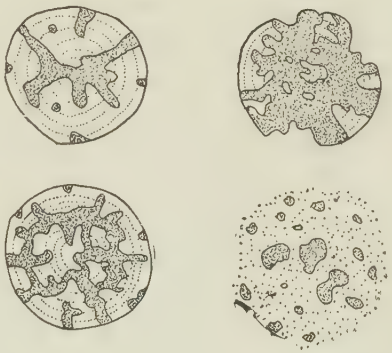


FIG. 142. Digestion of starch grains by diastase. The four figures show successive stages of digestion by the enzyme, diastase. (Redrawn from Strasburger.)

Let us consider a specific case of digestion as it takes place in the germination of a wheat grain. Starch grains occur in the endosperm cells of the grain. The starch is insoluble in water and cannot diffuse from cell to cell. After the grain has absorbed water and cellular activity has begun there is secreted an enzyme (or mixture of enzymes) called **diastase,** which has the property of changing starch to glucose. Thus, in the storage cells of the endosperm, starch is changed to glucose, a substance which is soluble and readily diffusible. The sugar diffuses from cell to cell, finally reaching the growing points of the embryo where it is used in growth. Other enzymes digest insoluble fats or proteins in the seed.

Not only in seeds, but throughout the plant wherever insoluble

foods are stored, the process of digestion occurs. For example, when a potato tuber sprouts, the growth of the sprouts is preceded by digestion of stored food in the cells of the tuber. When buds on a twig expand and develop into new shoots or into flowers this activity is made mostly at the expense of insoluble food stored in tissue of the twig near the bud, and, preceding the movement of this food to the growing point of the bud, digestion takes place in the storage cells. Digestion is, in nature, a function of living cells. It is possible, however, to remove enzymes from the living cells which produce them and bring about digestion in a solution in a test tube in the absence of any living protoplasm.

Enzymes are substances, probably protein in nature, which are produced in living cells of plants and animals, and which resemble inorganic catalysts, such as platinum, in that certain chemical changes go on very rapidly in their presence but very slowly or scarcely at all when they are not present. They greatly accelerate the rate of many important changes in cells which otherwise would practically not go on at all. Also, owing to the presence of the proper enzymes, changes may go on in living cells at relatively low temperatures (below 40° C.) which would otherwise go on at the same rate only at such high temperatures as would be fatal to all living protoplasm. No enzyme has been secured in sufficient purity to determine its exact composition. The principal characteristics of enzymes may be summarized as follows:

1. They are produced by living protoplasm.
2. They may be separated from protoplasm and still retain their activity for years if stored under proper conditions.
3. They are effective in small quantities.
4. They are sensitive to heat; heating to 60° C. renders them permanently ineffective.

Not all enzymes are digestive enzymes. Zymase, produced by yeast cells, converts glucose into alcohol and carbon dioxide; and many different chemical changes brought about by enzymes are not of the nature of digestion.

Food Transfer.—Absorption of water, the secretion of enzymes, and digestion are but preliminary to the transfer of food from the storage cells to the growing parts of the germinating seed. Conductive tissue is poorly developed in the rudimentary plant or

embryo seed, hence transfer of material from one part to another must be almost entirely by diffusion from one living cell to another. From our discussion of diffusion in Chapter III we learned that any substance tends to diffuse from a region where there are more dissolved particles of that substance per unit volume of solution to a region where there are fewer particles of that same substance per unit volume. At the growing points of the embryo, soluble foods are being transformed into cellulose walls and into protoplasm, and

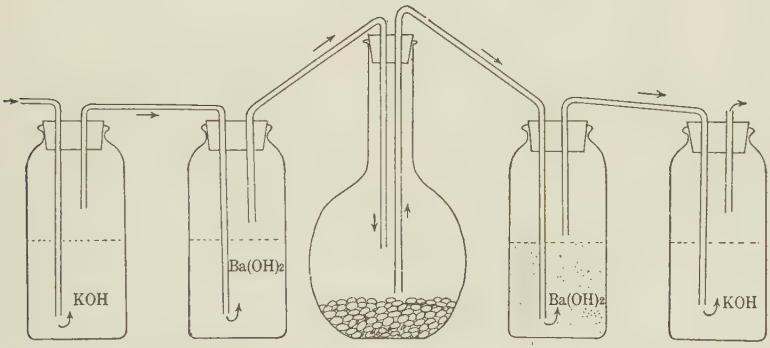


FIG. 143. Diagram of apparatus used to demonstrate the evolution of carbon dioxide from actively respiring seeds. Air enters the apparatus by the tube at the left and passes through in the direction shown by the arrows. As the air bubbles through the solution of potassium hydroxide (KOH) in the first bottle the carbon dioxide gas in the air is absorbed by the solution, potassium carbonate being formed and remaining in the solution. The air is next passed through a solution of barium hydroxide $Ba(OH)_2$ to show whether all the carbon dioxide has been absorbed by the KOH solution. If the carbon dioxide had not been completely removed a white precipitate of barium carbonate would be formed. The absence of any such precipitate shows that the air passing into the flask containing germinating seeds is free of carbon dioxide. The evolution of carbon dioxide by the seeds is shown by the formation of the white precipitate of barium carbonate ($BaCO_3$) as the air from the flask is drawn through the next bottle. The KOH bottle at the right serves to prevent any carbon dioxide from passing in the reverse direction.

are thus being removed from solution. Hence a constant reduction in the concentration of soluble foods is going on at the growing points. The direction of movement of soluble foods is toward these points of relatively low concentration of such substances, and away from the parts of the seed (storage regions) where soluble foods are being produced by the action of enzymes upon the insoluble stored food.

Assimilation.—This is the final step in the utilization of the stored food. It is the transformation of the digested foods into

the living substance, protoplasm, and of certain of these foods by the protoplasm into cell walls. The change from dead to living matter may be said to be the most important and most interesting which takes place in organisms. We know almost nothing about the process, however, for an understanding of it would necessitate our first learning much more than is now known of the actual nature of protoplasm.

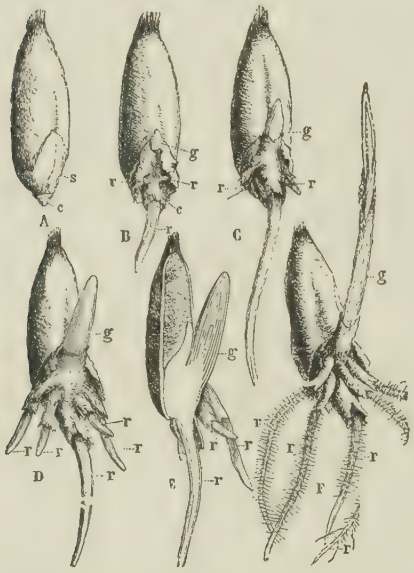


FIG. 144. Stages in the germination of wheat. *c*, coleorhiza; *g*, coleoptile; *r*, roots; *s*, embryo. (After Bocquillon.)

Respiration. — Respiration goes on more actively in germinating seeds than in almost any organ or tissue of green plants. That germinating seeds respire actively is shown not only by the large quantities of carbon dioxide given off, but also by the heat liberated in the process. For example, a large mass of germinating barley grains, or other seeds which germinate rapidly, actually may produce so much heat that they feel warm to the hand. If seeds with a high moisture content are stored in bulk, the heat generated from respiration may raise the temperature to the point where it is injurious to the seed. It will be recalled that respiration is an energy-releasing process in which part of the food is broken down into very much simpler compounds. This released energy is in part used by the seedling plant in the work of building up the complex compounds, other than carbohydrates, which the plant needs for its growth. Much of it, however, is dissipated as heat.

Growth.—The swelling of the seed, due to imbibition of water and to growth, is followed by the bursting of the seed coats. This rupture may be caused by the radicle, as in many dicotyledonous plants, or by the cotyledon, as in many monocotyledons. Freed from the seed coats, supplied with water and dissolved foods and with oxygen for respiration, the embryo now grows actively. Its growth

is due (1) to the enlargement of cells in the embryo, which are already formed, and (2) to the production of new cells at the growing point of the radicle and the plumule. The radicle is usually the first embryo structure to protrude from the seed. It grows downward, sends out branches, develops root hairs, and thus increases its absorbing surface.

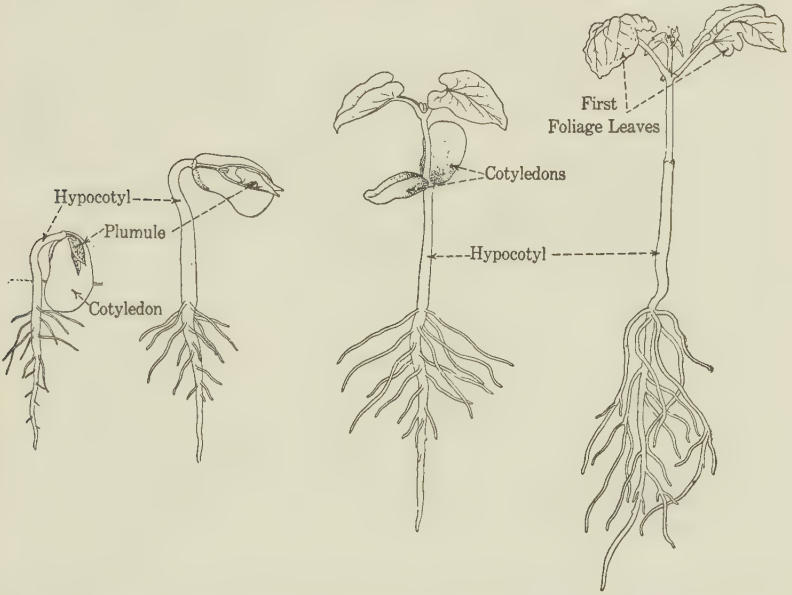


FIG. 145. Stages in the germination of the seed of common bean (*Phaseolus vulgaris*).

In many plants, such as the common bean, sunflower, and squash, the cotyledons and plumule are brought up to the light by the growth of the hypocotyl, and the seed coats generally remain in the soil. In oaks and in other plants, such as garden pea and scarlet runner bean, the cotyledons remain below the ground. In the cereals the one cotyledon (scutellum) does not even emerge from the seed. After the young plant reaches the light and develops chlorophyll-bearing tissue, it is no longer completely dependent upon the store of reserve food within the seed, but is now able to carry on photosynthesis.

CONDITIONS AFFECTING THE VITALITY OF SEEDS

Many seeds planted under the most favorable conditions for germination may fail to germinate. Some are quick to germinate and

form vigorous seedlings; others sprout but slowly, and the young plants are weak and lacking in vigor.

Many factors affect the vitality of seeds, that is, their capacity to germinate and produce seedlings capable of developing into adult plants. Seeds from strong, vigorous parent plants usually have

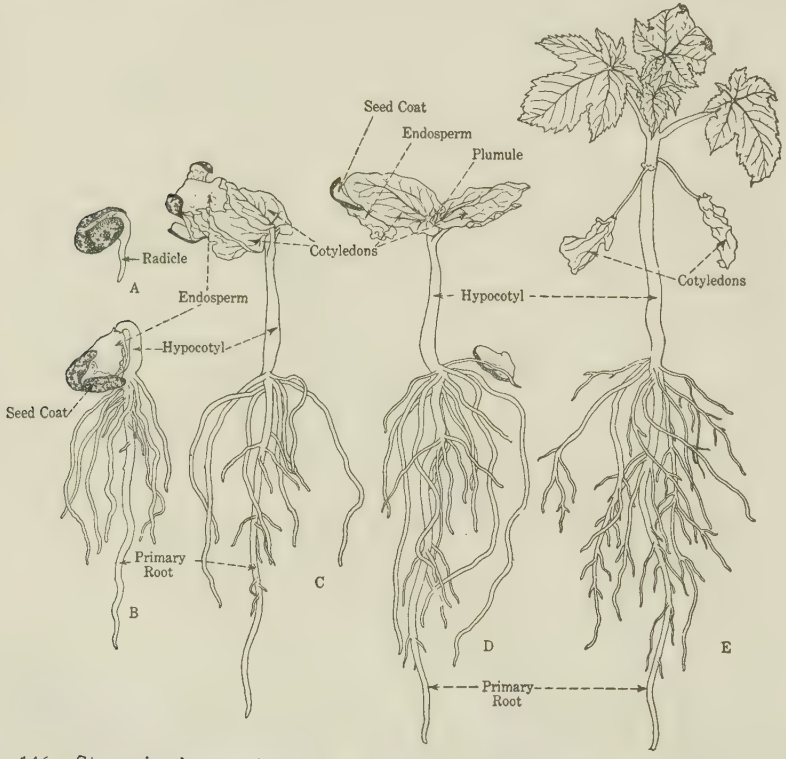


FIG. 146. Stages in the germination of a seed of castor-oil plant (*Ricinus communis*).

larger embryos and a greater amount of stored food than those from weakly parent plants. The vitality of the seed is influenced by the temperature of the air and the amount of moisture in the air at the time the seed is maturing. Most seeds mature best under dry atmospheric conditions, and with moderately high temperature. Seedlings are usually most vigorous when grown from seeds which have been allowed to reach full maturity on the plant. Conditions under which seeds are stored influence their vitality. Low temperatures and low humidity of the surrounding air are desirable to prevent germination during storage and to retain the vitality of the

embryos. It is well known that seeds gradually lose their vitality as they grow older. As a rule, seeds containing much oil, such as those of corn and flax, lose their vitality much more quickly than seeds containing little oil, such as those of legumes.

Various organs of the plant may exhibit dormancy, that is, a period during which they do not grow. It is best shown in seeds, although bulbs, tubers, buds, and spores also have a dormant or resting period. Most seeds lose their vitality in 5 or 6 years. However, the seeds of some legumes have been known to retain their vitality for 50 to 80 years. Recent studies of Indian lotus (*Nelumbo nucifera*) fruits which had lain buried in a peat bog for more than 200 years showed a very large percentage of the seeds to be still capable of germination. However, there is no reason for believing any of the frequent reports that the seeds placed in Egyptian tombs thousands of years ago are still capable of germination. The conditions under which seeds are stored determine their longevity. Most favorable conditions are fairly low and uniform temperature and relatively low atmospheric humidity.

DORMANCY OF SEEDS

Many seeds are incapable of germination immediately after they mature, even though placed under the most favorable conditions. This characteristic is known as **dormancy** or **delayed germination**, and the causes vary in different types of seeds. Probably the most common cause is an impervious seed coat which prevents or retards the absorption of water. This is often the cause of dormancy in the seeds of legumes, such as alfalfa, sweet clover, etc. In a planting of such seeds, some will germinate in several weeks; some will remain in the ground for an indefinite period without germinating. The permeability of leguminous seeds and therefore the promptness with which they germinate can be increased by "scarifying," that is, passing them through a machine that scratches the surface of the seed coat. Another cause of dormancy is the inability of the embryo to break the seed coat. This is true of the common pigweed seed. As the seed lies in the ground, successive freezing and thawing, and the action of bacteria and fungi in the soil, gradually soften the coats and make germination possible. Still another cause of seed dormancy is the inability of the embryo to germinate until it has gone through a series of changes known as "after-ripening." This process may be hastened in some cases by exposure of the seeds to low temperatures.

SEEDLINGS

We have seen that in the germination of the seed the embryo grows, the seed coat bursts, and the seedling emerges. For a time, the young plant is wholly dependent upon food stored within itself or within the endosperm, with which it may maintain contact for a time. Not until the plant reaches the light and is thus able to manufacture its own food does it become independent. From the time when the young plant emerges from the seed coats to the time when it becomes entirely dependent upon food manufactured by itself it is called a **seedling.**

The life of a seedling is a precarious one. Its tissues are tender, and its surfaces usually not well protected from loss of water; the root system is not well established; there is danger of starvation should its reserve food supply be consumed before it reaches the light, a condition which may arise if seeds are planted too deeply, or the soil becomes crusted, thus preventing the seedling from reaching the surface.

Seedlings may be divided into two quite distinct types:

1. In the first of these types the cotyledon or cotyledons are raised above the ground by the lengthening of the hypocotyl. Some of the stored food in the cotyledons is used by the developing root, but a considerable quantity remains, and, before this is exhausted, the cotyledons, which are now in the light, become green and carry on photosynthesis to some extent. As the foliage leaves formed by the plumule gradually develop and take on their functions, the remainder of the reserve food is used up, and the cotyledons shrivel. A familiar example of this type of seedling is the common bean (*Phaseolus vulgaris*).

2. In the second type of seedling the cotyledon or cotyledons remain beneath the ground, and the hypocotyl undergoes little or no elongation. This type is illustrated by wheat and all other grasses. The cotyledons remain within the seed coats and in species lacking endosperm serve as food-storing organs only.

In seeds with endosperm the cotyledons serve as food-absorbing organs for the embryo. In seedlings of the first type the cotyledons may serve temporarily as photosynthetic organs, after the endosperm has been used up.

CHAPTER IX

RELATION OF THE PLANT TO ENVIRONMENT

The various external conditions or factors which influence the development, structure, and activities of the organs of the plant are collectively spoken of as the **environment.** The environment is a complex set of factors.

It is convenient to classify the environmental factors into three groups:

1. **Climatic factors,** those which act upon the plant through the atmosphere.
2. **Edaphic factors,** those which act through the soil.
3. **Biotic factors,** those arising from the presence of other plants and animals.

Some of the principal factors in each of these three groups are:

Climatic factors:
- Temperature.
- Light.
- Carbon dioxide concentration.
- Atmospheric humidity and precipitation.
- Wind.

Edaphic factors:
- Available water in the soil.
- Air in the soil.
- Temperature of the soil.
- Quantity and nature of the soil solutes.

Biotic factors:
- Competition among different species of plants.
- Grazing by animals.
- Soil bacteria, algae, and protozoa.
- Parasitic fungi.
- Insects that injure plants.
- Insects that pollinate.

TEMPERATURE

Each of the physiological processes—respiration, absorption, carbohydrate synthesis, digestion, reproduction, growth, etc.—is carried on between certain temperature limits (maximum and minimum). Somewhere between these two there is a temperature (the optimum) at which the process goes on most actively.

The minimum, optimum, and maximum temperatures for one process may differ considerably from those of another process taking place in the same plant. For example, in many plants absorption by roots can take place at somewhat lower temperatures than the minimum temperatures for reproductive processes in the flower. Moreover, in any given process, such as photosynthesis, absorption, etc., the minimum, maximum, and optimum temperatures may vary rather widely in different species. These differences between species in their temperature relations are of great importance in determining what plants shall or shall not grow in a given region or at a given altitude. In the United States, for example, cotton is not grown profitably north of the line where the average summer temperature is below 77° F. The commercial apple-producing regions do not extend south of the line of 79° F. mean summer temperature.

Resistance of Plants to Low Temperatures.—It is well known that some plants will withstand a much lower temperature than others. For example, the date palm is usually injured by temperatures below 20° F., whereas most varieties of apples will endure temperatures much below zero, if the tissues are mature and in a dormant condition.

The causes of freezing injury to plant cells are not fully understood. It is known that in freezing there is a rapid withdrawal of water from the cells, judging from the fact that ice crystals form in the intercellular spaces. Thus there would result a dehydration of the protoplasm. However, it is the view of certain workers that injury to the cell from freezing is not due to dehydration, but rather to mechanical disturbances which have a disruptive effect upon the structure of the protoplasm.

In some plants which are very resistant to injuries due to low temperatures the protoplasm is relatively less sensitive to injury attending ice formation. In other plants, resistance is undoubtedly

due to certain substances, as sugar, which are present in the cell sap in such quantities as to prevent freezing of the water in the protoplasm except at very low temperatures. Plant parts whose protoplasm is relatively low in water content (seeds, for example) can withstand very low temperatures without injury. Often young shoots whose living tissues contain much water are killed by frost though older stems whose cell sap is more concentrated may survive.

Gardeners commonly practice the process of "hardening" their transplants. A tomato plant, for instance, which is removed suddenly from a warm greenhouse in the spring to the garden out-of-doors has little resistance to low temperatures, and the death point (temperature at which it will be killed by cold) is relatively high. The usual procedure is to move the plants from the greenhouse to a cold-frame where the temperatures are intermediate between those of the greenhouse and out-of-doors. After remaining for a time at these intermediate temperatures the plants may be planted with safety in the open.

LIGHT

By the term light we mean to include all the energy (radiant energy) which reaches the plant from the sun. Light affects the plant and its activities in many ways, as follows:

1. The plant derives from light the energy which it stores up in potential form in its food; the photosynthetic process goes on only in the light.

2. Much of the light energy absorbed by the plant is transformed to heat energy, thus raising the temperature of plant tissues. This elevation of the temperature in turn influences the rate of different processes going on in the plant. For example, transpiration may be increased through heating of the leaf due to absorbed light.

3. Light influences the position of plant organs. The leaves of shade plants are almost always more or less horizontal so that light falls upon them at right angles to their surface. The leaves of some sun plants hang down or are held more or less perpendicular so that the sun's rays, much of the time, strike the leaf surface at an acute angle. Thus, much less radiant energy is absorbed by the leaves.

4. The intensity of light and its duration affect the rate of growth

and development of plants, and particularly their flower production. There is evidence in the case of certain crop plants that the development of flowers is dependent not so much upon the intensity of light as upon the relative length of day and night. Some plants which flower only during the long days of June can be made to bloom in mid-winter, if the length of daily illumination is increased by means of electric lights. Other plants which normally bloom and fruit in the autumn, when the days are short, can be made to bloom and fruit in mid-summer, if the length of day is shortened by placing them in the dark for a part of each day. The development of plants in relation to the length of daily light period is a phenomenon termed **photoperiodism.**

FIG. 147. Two potato plants, *A*, grown in the light, and *B*, grown in the dark. The two plants have the same number of internodes. A plant such as *B*, which has been grown in darkness, is white or yellow in color, has much longer internodes than a normal plant and has very much reduced leaves. Such a plant is said to be *etiolated.* Etiolated plants cannot continue to grow after the food in the tuber, bulb or seed from which they have developed has been exhausted. (After Pfeffer.)

5. Light may modify the form of the plant. Intense light seems to have a stunting effect. This may be the principal cause of the low stature of alpine plants, although other factors, chiefly low temperatures, and possibly high rate of transpiration, may play a part. Trees in the open branch profusely, whereas the same species in the forest, where the light from the sides is largely cut off, grow taller and produce fewer branches.

6. The form and internal structure of leaves are markedly influenced by light. This influence is well shown in the great differences in the internal structure of the leaves of sun and shade plants. The following are the principal anatomical characteristics of the leaves of sun plants and shade plants.

SUN PLANTS	SHADE PLANTS
Thick palisade parenchyma due to increase in length of cells or in number of layers of cells.	Thin layer of palisade tissue or none at all.
Spongy parenchyma not well developed.	Well-developed spongy parenchyma.
Thick leaves.	Thin leaves.
Small intercellular spaces.	Large intercellular spaces.
Thick and heavily cutinized epidermis.	Thin and slightly cutinized epidermis.
Stomata confined to lower side or more abundant on the lower side.	Stomata on both sides, the number on the two sides nearly or quite the same.
Frequently smooth and shiny surfaces, capable of reflecting much of the light falling upon it.	Generally dull surfaces.
Often densely hairy.	Seldom very hairy.

Some of these differences, particularly in internal structure, are frequently found between different individuals of the same species which are growing respectively in sunny and in shaded habitats.

CARBON DIOXIDE

Carbon dioxide is a raw material used in photosynthesis; consequently, as a factor of the environment it is of very great importance. However, under natural conditions the supply of carbon dioxide is quite uniform, and there are no recognizable differences among plants growing naturally which can be attributed to variations in this factor.

It is of interest to note that, by artificially increasing the supply of carbon dioxide above the 3 parts in 10,000 generally present under natural conditions, the production of food and the rate of growth of the plants may be increased. This fact has been shown

to be of practical importance in the growth of vegetables and other plants in commercial greenhouses when a cheap source of carbon dioxide is available.

FIG. 148. Timothy plants grown under different lengths of day, as indicated by number of hours on the containers. The control plant (*C*) was grown under natural length of day. Photographed July 1, 1931. Heads were first found on a length of day of 13½ hours, this being the shortest which was favorable to heading. (Photograph furnished from Journal of Agricultural Research, Vol. 38, No. 7, 1934, article by Evans and Allard.)

PRECIPITATION AND ATMOSPHERIC HUMIDITY

Precipitation.—This is a factor second in importance only to temperature in determining the distribution of different plants in the various regions of the earth. The great climatic plant formations of the world are woodland, grassland, and desert. Which type will dominate in any part of the world is determined largely by the amount and distribution of the rainfall. It is not so much the total amount of rain falling throughout the year as the distribution of the rain over the whole year which determines what kind of plants will grow in a given region. For example, in the tropics where the rainfall is heavy and rather uniformly distributed throughout the year, the dominant vegetation is an evergreen forest; on the other hand, in those parts of the tropics where the total rainfall for the year is equally heavy but occurs during a few months of the year, the forests are chiefly of the deciduous type.

Atmospheric Humidity.—The humidity of the air surrounding the plant is the most important single factor in determining the rate of transpiration. Low humidity is often assumed to be principally responsible for the various devices which plants seem to employ to reduce transpiration. (See discussion of transpiration, Chapter VI, pages 145-150.) However, other things being equal, it is not the percentage of water vapor in the atmosphere which determines how rapid transpiration shall be. It is, instead, the percentage of water which the air can still absorb before saturation is reached. With a given percentage of water in the atmosphere, this quantity increases with increase in temperature.

Even in the driest regions some water is always present in the air in the form of gas (water vapor). When the air contains all the water vapor it can hold, it is said to be saturated, but the percentage of water in a saturated atmosphere varies widely with the temperature. Air which is saturated when it is at a low temperature will be far from saturated at a considerably higher temperature, for with rise in temperature its capacity for holding water vapor increases. Air saturated at a relatively high temperature loses some of its water vapor when it is cooled. When that occurs, small drops (mist or fog) or larger drops (rain) are formed, but the air remains saturated at the lower temperature. Any subsequent increase in temperature, however, results in the air becoming less than saturated, unless it absorbs water meanwhile from free water surfaces.

WIND

One of the principal, although indirect, effects of wind on plants is increasing the rate of transpiration. Aside from the indirect effects of wind upon the plant, there are various direct effects. Thus in locations where there are strong prevailing winds the trees are generally smaller than in other localities, frequently the trunks are bent away from the wind, and often the branches on the windward side are almost entirely suppressed so that the tree has a one-sided form. Certainly the deformations of the exposed trees on sea coasts and on mountain tops are largely due to strong winds, though in the latter case the weight of the winter snow accumulated on the branches is also an important factor.

AVAILABLE WATER IN THE SOIL

By far the most important of the environmental factors which have to do with soil (edaphic factors) is the supply of soil water available to the roots of plants. We shall enumerate the principal factors determining the quantity of available water and mention some of the effects upon the plant of differences in the quantity.

Principal Factors Influencing the Available Water in the Soil.—

1. The amount of annual precipitation.
2. The distribution of precipitation over the year.
3. The humidity of the atmosphere, since it affects the rate of water loss from the soil by evaporation.
4. The distance of the water table (level of standing water in the soil) below the surface of the soil. The fluctuations in this from one season to another depend chiefly upon the precipitation and evaporation.
5. Rate at which water percolates downward into the soil. This is most rapid in sandy soil, and progressively slower in clay and humus.
6. The power of the soil to raise water from lower levels (the water table) by capillarity. Water is raised much higher by capillarity in clay soil than in sandy soil, but it rises at a more rapid rate in sandy soils than in clay soils.
7. Vegetation. Plants growing in soil may greatly decrease the amount of water in the soil. Because of the water absorbed by the roots and lost by transpiration from other plant organs, the soil may lose water much more rapidly than if it were bare.

The importance of the available water in the soil is so great in its effect upon plants that botanists are accustomed to classify plants, as regards their relations to environment, on the basis of their water requirements. They recognize:

1. **Xerophytes.**—Plants which are very resistant to drought or live in very dry places, for example, Russian thistle (*Salsola*), millet (*Setaria italica*), sorghum (*Andropogon*), cactus (*Opuntia* and other genera), sagebrush (*Artemisia*).

2. **Hydrophytes.**—Plants which live in water or in very wet soil, such as cattail (*Typha*), water lilies (*Castalia, Nelumbo*), sedges (*Carex*).

3. **Mesophytes.**—Plants growing best with moderate water supply: the common plants of meadow and forest.

4. **Halophytes.**—Plants able to grow in salt marshes and alkali flats where there may be an abundance of water in the soil but where, because of the high concentration of the soil solution, water is absorbed with difficulty. Examples are greasewood (*Sarcobatus*), salt bush (*Atriplex*), sugar beet (*Beta*), glasswort (*Salicornia*).

AIR IN SOIL

The quantity of air in the soil is of considerable importance to plants growing in it. The living cells of the root must have oxygen in order to respire. Respiration is particularly active in the cells of the growing points and the actively growing regions near them. Normally the roots secure the necessary oxygen for respiration by its diffusion into the roots through the root hairs and ordinary epidermal cells. A moderately dry soil, not excessively fine in texture, contains much air in its pores. A very wet soil contains less air than would the same soil in a drier condition, for part of the space (that of the larger pores) which would be occupied by water in the wet soil is occupied by air in the drier soil. In a water-soaked soil there is practically no air save that which is dissolved in water. As a rule, the larger the soil particles and the looser and more porous the soil, the better its aeration. Most plants die if the soil about their roots is continuously water-soaked. Their death is presumably due principally to insufficient oxygen supply. There are some plants, however, which can thrive although the root system is submerged in water or surrounded by a soil which is water-soaked. Almost all such plants contain in the stem and root large communicating air spaces. Thus air absorbed into the leaves and stems may reach the living cells of the root in sufficient quantity. Some, like the bald cypress (*Taxodium distichum*) and various species in tropical mangrove swamps, produce special root branches which grow upward until their ends are above the water level. These special root branches have a central core of loose parenchymatous tissue through which air is said to pass downward to the submerged parts.

SOIL TEMPERATURE

The temperature of a soil may greatly influence the plants which grow in it. One of the principal effects of low soil temperature is the reduction of the rate of water absorption by the root. Plants whose roots are in a soil containing abundant water may wilt when the temperature is very low.

There are a number of factors which affect the soil temperature. Among the most important of these are: (1) **The intensity and duration of the light which falls upon the soil.** (2) **The air temperature above the soil.** (3) **The amount of water in the soil.** (A wet soil is generally cooler than a dry soil.) (4) **The color of the soil.** (Dark soils absorb heat more readily than light-colored soils.) (5) **The presence or absence of a living or non-living cover.** (Such a cover retains heat but slows down the absorption of heat.) (6) **The physical nature of the soil.** On a north exposure the soil is naturally cooler than on a south exposure because of the smaller quantity of sunlight which it receives.

QUANTITY AND NATURE OF THE SOIL SOLUTES

Water absorption by the roots can take place only if the concentration of the cell sap of the root hairs is greater than that of the soil solution. The adaptations of plants growing naturally in salt marshes or in so-called alkali soils resemble those of plants growing in very dry soils or in an atmosphere of very low humidity. If the root systems of most plants were exposed to such concentration as exists in salt swamps, and strongly "alkali" soils, they would not be able to absorb sufficient water to replace that lost by transpiration and would soon die.

The soil water of some soils is deficient in one or more of those essential elements which the plant must secure from the soil. These elements, it will be recalled, are potassium, calcium, magnesium, iron, nitrogen, sulphur, and phosphorus. Plants growing in such soils have their growth rate much reduced and remain dwarfed.

Most seed plants thrive best in a slightly acid soil but there is a wide variation in the tolerance of different plants for acid and slightly alkaline soils. Certain plants, such as sour dock (*Rumex*

acetosella) and heather (various *Erica* species), growing normally on quite acid soils, do not thrive in soils which are rich in lime. This is probably due to the fact that such soils are not sufficiently acid.

THE INFLUENCE OF CERTAIN BIOTIC FACTORS UPON PLANTS

Other species of organisms, both plants and animals, are as much a part of the environment of a given plant as are the various climatic and edaphic factors which we have mentioned above. Though in general these biotic factors are secondary to the factors which have to do directly with soil and atmospheric conditions, they are often of great importance, and sometimes (for example, in the case of certain plant parasites) of greater importance than any other factor in determining whether given individuals or species shall survive in a certain locality.

In nature, plants compete for space, light, water, and inorganic salts. Ordinarily water is lost more rapidly from soil covered with plants than from bare soil. As the result of the competition of plants for the water in a soil, certain species may die off because of excessive drying of the soil by other species which absorb water more rapidly. In a similar manner, there is competition in a forest for light, and the dense shade of the larger plants may prevent the growth of smaller plants which would grow in the locality if it were not for the shading. On the other hand, certain plants which grow well beneath the trees of the forest because the temperature is relatively low there and the humidity high would not be able to grow in that locality if the trees were removed.

Grazing by wild or domestic animals may greatly affect the plants growing in a certain habitat. Most species are unable to survive the constant removal of leaves and parts of the stem by grazing animals. As a result, those plants (principally certain grasses) which are able to withstand cropping and to spread without seed formation tend to take full possession of a closely grazed piece of land.

Uncontrolled grazing on the millions of acres of range lands in the western United States has greatly depleted their grazing capacity. As a result of the overgrazing, not only have the more palatable grasses lost their vigor and productive capacity, but less desirable plants have taken their place, and much of the depleted area has suffered seriously from erosion. In many sections the original plant covering is greatly modified, and in its place the vegetation stand

is composed of a high percentage of introduced species and of native species which have assumed the rôle of weeds.

The soil itself contains many simple organisms, such as algae, bacteria and other fungi, and protozoa. Some of these, particularly certain of the bacteria, raise the fertility of the soil by increasing the amount of nitrogen available for the seed plants growing in it. In the absence of certain of these organisms, plants belonging to the bean family (Leguminosae) remain stunted. Other organisms in the soil may be injurious to seed-bearing plants either because they lessen soil fertility (some of them greatly reduce the available nitrogen) or because they are the cause of root diseases.

Parasitic organisms, bacteria and other fungi, nematode worms, and insects are biotic factors of very great importance. The insect parasite, *Phylloxera*, which at one time destroyed most of the French vineyards, the fungus parasite causing chestnut blight, which has killed many of the chestnut trees of the United States, and the parasitic fungus responsible for the white pine blister rust, a plant disease which has caused great losses of the white pines of the eastern United States, are particularly striking illustrations of the importance of parasitic plants and animals as living factors in the environment surrounding plants.

TRANSFORMATION OF MATERIALS AND ENERGY BY THE PLANT

Plants are composed of matter, and they absorb, store, and transform energy. Their very existence is dependent upon an exchange and transformation of materials and energy. Plants expend energy and do work. If it were possible to take moving pictures of all the parts of a growing plant, the film would show the roots twisting and turning and making their way between the soil particles. The young sprout of the germinating seed would be shown penetrating the soil or lifting the load of soil from its path, and we could see the movement of the parts of opening buds. In fact, there is movement throughout the plant body, although the rate of movement is generally slow. And if we examine the interior of the cells, we see the living material, the protoplasm, moving in streams from place to place in the cell. Thus plants, just as truly as animals, actually

do work as long as they are alive, and this work requires a supply of energy.

Mention has already been made of the fact that if it were not for green plants none of the animals or chlorophyll-free plants in the world could exist. This is true because, with the exception of a few kinds of bacteria, the chlorophyll-free plants and the animals

FIG. 149. Tomato leaves showing, on the right, a leaf from a plant supplied with a sufficient quantity of all the necessary minerals, and, on the left, a leaf showing spotting and other abnormalities characteristic of plants grown under conditions which were the same except that the supply of potassium was deficient. (After Johnston and Hoagland.)

are incapable of building up from the simple compounds in the soil and atmosphere the complex compounds of which their bodies are constructed. The formation of these complex compounds, or foods, constitutes the great rôle of green plants in organic nature. The making of foods by plants is of very great significance for two reasons:

1. Because these foods furnish the material out of which the bodies of plants and animals are constructed.

2. Because, in the making of these foods, energy from the sun, which is the world's great source of energy, is stored, and this stored

energy can be released within the bodies of the living organisms which make or use the food. The energy thus secured is the only energy which animals or non-food-making plants can use for their life processes. In green plants it is the only energy which can be used for any process except carbohydrate manufacture. Since green plants are responsible for important transformations (1) of materials and (2) of energy, it is fitting to summarize here these changes in material and energy.

The Material Which Green Plants Absorb and the Changes Which These Materials Undergo.—The principal substances which are taken into the green flowering plant in considerable quantity and which are essential to its proper development are as follows:

From the soil:
- Water.
- Salts, containing the following elements:
  - Nitrogen—principally as nitrates but in some cases as compounds of ammonia.
  - Phosphorus—as phosphates.
  - Sulphur—as sulphates.
  - Potassium, Calcium, Magnesium, Iron } In combination with one of the three preceding elements.

From the atmosphere:
- Carbon dioxide.
- Oxygen.

The principal changes which these substances undergo in the plant will be briefly stated.

Water.—The water used in the process of photosynthesis is transformed, that is, it ceases to be water and becomes part of the carbohydrate, glucose. The water which passes from the plant during transpiration in the form of vapor is changed only in its physical form and not (chemically) into another compound. During the process of respiration sugars are broken down and water is formed again.

Nitrogen, Phosphorus, and Sulphur.—These elements are particularly important as the raw materials, together with soluble carbohydrates, of the proteins and of the amino acids from which

proteins are built up. Proteins contain 15 to 19 per cent of nitrogen and ½ to 1½ per cent of sulphur. It is said to be chiefly in the leaves that inorganic nitrogen is elaborated into amino acids and other nitrogenous organic compounds. Phosphorus is found in some proteins, particularly the nucleo-proteins of the nucleus, which contain 0.3 to 3 per cent of that element.

FIG. 150. Photograph showing a boron-deficient tomato plant (left) and one grown in a similar solution to which 0.55 part per million of boron as boric acid had been added (right). (From Johnston and Dore.)

Potassium, Calcium, Magnesium, and Iron.—Though all the higher plants must be supplied with these substances, we have little knowledge of the changes which the simple inorganic compounds of these elements undergo within the plant. Part, at least, of the magnesium is used in the making of chlorophyll *a* and chlorophyll *b*.

Iron is essential to chlorophyll formation, although the chlorophyll molecule contains no iron. Iron is also believed to act as a catalyst

FIG. 151. A comparison of greenhouse-grown tomatoes in fertile soil, in sand to which nutrients were added, and in water to which nutrients were added. There were no essential differences in the performance of the plants under these three different conditions. (From Hoagland and Arnon.)

in the oxidation processes of plant respiration. It may be that potassium, calcium, and iron perform their essential functions without

change from the simple inorganic form in which they exist in the soil solution.

Carbon Dioxide.—Carbon makes up 40 to 50 per cent of the dry weight of all plants, and the gas carbon dioxide is the source of all this carbon. The carbohydrates are utilized in the making of proteins and fats. When sugars and fats, which are the principal respirable materials in the plant, are respired, carbon dioxide is again formed and liberated into the atmosphere. When plant parts die, the sugars, starch, cellulose, fats, and all other organic compounds are broken down by bacteria and other fungi, and the carbon is finally set free from these compounds in the form of carbon dioxide. Thus there exists in nature a carbon cycle in which the carbon of carbon dioxide is continuously being built up into complex foods, which are again broken down with the formation of carbon dioxide. Green plants, animals, and bacteria and other fungi may all play a part in this carbon cycle.

FIG. 152. Water-culture jar used by the plant physiologist Sachs in the middle of the last century. (After Hoagland and Arnon, reproduced from Sachs, *Lectures on the Physiology of Plants*, Clarendon Press, 1887.)

Oxygen.—Carbohydrates, protein—in fact, all essential substances in the plant—contain oxygen in combination with other elements. This oxygen is derived for the most part from water or from carbon dioxide used in photosynthesis. But the plant also absorbs the free oxygen of the atmosphere. This is utilized solely for the oxidation of sugars and fats in respiration and becomes part of the compounds produced by respiration.

In addition to the ten elements—carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, magnesium, calcium, and iron—long recognized as essential to the continued growth and development of green plants, there are certain other elements which are known to be beneficial or absolutely indispensable to some plants. For example, it has been found that manganese, boron, copper, and zinc are essential to the growth of a number of different kinds of green plants, but that very small amounts suffice. Our failure

to recognize earlier that certain of these elements are essential is due to two facts. First, they are needed only in extremely small quantities, and second, the "chemically pure" compounds or the ordinary distilled water used in preparing culture solutions in the past have generally, or at least frequently, contained unsuspected traces of these elements quite sufficient in quantity to supply the needs of the plant's growth in culture.

FIG. 153. An illustration of the water-culture technique for studying the nutritional responses of lettuce plants under controlled conditions. The individual plants are supported in corks which are placed in holes drilled in the metal covers. The glass and rubber tubes carry air under pressure, which is bubbled through the nutrient solution in the tanks. (From Hoagland and Arnon.)

The rôle of the mineral elements, including nitrogen, derived from the soil has been learned chiefly through experiments using solution and sand cultures. In solution cultures appropriate salts are dissolved in distilled water. The plants are grown with their roots in the solution. It is possible with this technique to arrange various combinations and concentrations of the mineral elements, and to observe the effects upon the behavior of plants. Moreover, by omitting from the solution any particular element, the deficiency symptoms can be observed. So-called sand cultures involve the use

of nutrient-free pure quartz sand to which is added various solutions. The water-culture method for growing plants without soil has recently received considerable attention by commercial as well as amateur gardeners. This method of growing plants is also recently described under such names as "tray agriculture," "tank farming," "soilless gardening," and "hydroponics." However, the method is not new, for as early as 1860 the German plant physiologist, Sachs, successfully grew plants in nutrient solutions. The water-culture installation employed by Sachs is shown in Fig. 152, and his standard solution formula was as follows:

KNO_3	1.00	gram	per	1000	cc.	of	water.
$Ca_3(PO_4)_2$	0.50	"	"	"	"	"	"
$MgSO_4$	0.50	"	"	"	"	"	"
$CaSO_4$	0.50	"	"	"	"	"	"
NaCl	0.25	"	"	"	"	"	"
$FeSO_4$	Trace.						

Since Sachs' early work, a number of different solution formulas have been employed by various workers. It should be emphasized that the chief use of the water-culture technique at present is for studying the nutritional responses of plants under controlled conditions. Commercial application to large-scale production is beset with many difficulties which may be successfully overcome as knowledge and experience are extended.

Other elements concerning which there is some evidence indicating their importance to particular plants are: **silicon, sodium, chlorine, aluminum, bromine,** and **iodine.**

Recently, it has been determined experimentally that the element molybdenum is also an essential element for certain higher plants. For example, when tomato plants were grown from the seedling stage in rigidly purified nutrient solutions which contained all the eleven elements derived from the soil, regarded as essential, namely N, P, K, Ca, Mg, S, Fe, B, Mn, Zn, and Cu, within a few weeks the lower leaves disclosed a characteristic mottling. The deficiency symptoms were prevented from developing by adding 1 part of molybdenum as molybdic acid to 100,000,000 parts of the nutrient solution, or by spraying the plants with a dilute solution of molybdic acid. In the latter case, the leaves and stems of the

tomato plants absorbed enough molybdenum to supply them with their needs for this element.

Energy Changes Brought About by the Plant.—We have already learned that certain chemical changes, for example, burning and respiration, are attended by liberation of energy.

One of the principal rôles of green plants is to take certain of the simple compounds (carbon dioxide, water, and mineral salts) in which no available energy is stored and build them up into substances such as carbohydrates, fats, and proteins, in which there is stored or potential energy. It is the energy of sunlight which is thus stored by green plants. These substances produced by plants constitute the source of all energy which is used by animals within their bodies, and by chlorophyll-free plants. Moreover, if we except the energy of falling water and of the wind, and that of the tides and waves, which we may some time be able to utilize, all the energy which is used by man for any purpose is secured from the energy stored in the substances made by plants. Our principal fuels, wood and coal, are unmistakably plant products. All the explanations of the origin of petroleum agree that directly or indirectly it also has been produced by green plants. The energy set free in the form of heat when these fuels are burned can be changed into mechanical energy by the steam engine or gasoline motor. This in turn may be transformed into electrical energy by the dynamo, and this again into light energy by the electric lamp or into heat by the electric stove.

Fig. 154. Corn and sunflower plants grown in nutrient solution contained in 2-quart Mason jars. The plants are held in place by perforated corks, and the jars are covered with thick paper to exclude light. (From Hoagland and Arnon.)

By whatever form it may take, the energy secured by the combustion of coal, wood, or petroleum is but the energy of sunlight which perhaps hundreds of centuries ago was absorbed by green leaves when carbon dioxide gas and water were being united to produce the energy-storing substances from which these fuels were formed. Green plants are, then, unique, not only as makers of substances essential for the building and repair of the bodies of all organisms, but also as the storers of the sun's energy for use within the bodies of organisms, and for use in the industries. The amount of energy which can be secured from other sources than the combustion of the products of photosynthesis is only a small fraction of that used in industry. Accordingly, man is, and may always be, dependent upon green plants for much of the energy used in the industries, as he is also for all the energy used within his own body.

Thus the plant absorbs various materials from the outside world, and also energy from light. Its life is a series of chemical and physical processes. Absorption and conduction of materials, and transpiration are largely physical processes, whereas food manufacture, digestion, respiration, and assimilation are primarily chemical processes. Some of the chemical processes are constructive, and some are destructive. The constructive process, photosynthesis, involves the storage of energy; the destructive process, respiration, involves the liberation of energy. From the simple carbohydrate produced by photosynthesis and (in some cases) mineral substances from the soil, the plant constructs other plant foods (fats, proteins, etc.); and, finally, foods are transformed into protoplasm, a process known as assimilation, and into new cell-wall material. Involved in the food transformations are storage and digestion. The plant stores food in various organs, chiefly in roots, underground stems of various sorts, and in seeds. These stored foods are often insoluble, and before they can be moved from cell to cell they must be rendered soluble and diffusible, a process known as digestion.

CHAPTER X

THALLOPHYTA
ALGAE

CHARACTERISTICS OF THE THALLOPHYTA

The thallophytes include the simplest and the most primitive of plants. Although many of them are small and inconspicuous, still they are ever present, as are trees and shrubs and herbs. We are familiar with those that form a green, frothy scum on the water of ditches, ponds, reservoirs, and stagnant pools; and those that form a greenish slime on the sides and bottom of drinking fountains; and those that appear as a green coating on the north sides of trees in moist woods; and the great array of "seaweeds." We are also familiar with such fungi as bacteria, molds, mildews, yeast, smuts, rusts, and mushrooms. In size they vary from bacteria, many of which have a diameter of less than 1/2000 millimeter, to the giant brown seaweeds of our California coast, some of which may be several hundred feet long. Typically, the Thallophyta are aquatic plants, but most of the fungi, though preferring moist locations, do not thrive if submerged in water.

The name Thallophyta means thallus plants, a thallus being a plant body without true roots, stems, or leaves. There are, however, thallus plants in other divisions besides the Thallophyta; and in some plants belonging to the Thallophyta there are structures which resemble superficially the roots, stems, and leaves of the flowering plants and which perform the same functions, at least in part.

Reproduction in the Thallophyta (as in other divisions of the plant kingdom) may be either by the asexual or the sexual method. In the asexual method each new individual is the product of a single parent plant; in the sexual method each new individual develops from a cell (the zygote) which is the product of the fusion of two protoplasts generally originating in different parent individuals.

ALGAE
(THALLOPHYTA WHICH MAKE THEIR OWN FOOD)

Algae are universal in their occurrence. There is scarcely a moist situation that is without some kind of alga. They occur in and on the soil, on trees and walls, in still and running water, in fresh water and saline water; they may be free-floating, or attached; a number of different kinds live within the bodies of other organisms, plant or animal.

Algae make up the greater part of the vegetation of the ocean and lakes. The free-floating plants are generally unicellular forms and are spoken of collectively as the **phytoplankton,** plankton being a collective name for free-floating aquatic animals and plants. The innumerable microscopic aquatic animals are of great value as food for fish. Phytoplankton furnish the food for most of these aquatic animals, and thus indirectly form the basis of the food supply of fish. The importance of plankton may be judged by a study made of the fish-food resources of a typical lake—Lake Mendota, Wisconsin. It was estimated that the average amount of dry organic matter in a "crop" of plankton of this lake amounted to approximately 214 pounds per acre. The life of any individual organism which is a component of the plankton is short; hence there is a succession of crops of these microscopic organisms. Taking these into consideration, it was estimated, in the case of Lake Mendota, that the annual production of dry organic matter due to plankton would be 2568 pounds per acre.

Certain algae, chiefly blue-green and green, may accumulate to such an extent as to be undesirable. For example, they may form a greenish slime on the sides and bottoms of watering troughs and drinking fountains; or form a green, frothy, repulsive-looking scum on the water of ditches, streams, and ponds; or, in instances, become overabundant in reservoirs which are the source of drinking water. If large numbers of the algae in reservoirs are killed by very hot or very cold weather, their decomposition may give an unpleasant taste and odor to the water. Algae are readily destroyed by copper sulphate, even one part of the chemical in one million parts of water being toxic. Higher plants and fish are not injured by even larger concentrations of copper sulphate, nor is water so treated harmful to people who drink it.

The brown seaweeds, especially the large rock weeds and kelps, have been utilized as a source of fertilizer, chiefly because of their high potash content. They are also a source of iodine.

The substance agar-agar is obtained from a red seaweed common in Asiatic waters. In China and Japan it is a favorite food; in this country and Europe it is employed in making desserts, pastries, and ice cream; also in clarifying liquors and in canning fish. In Japan, China, and the Pacific Islands various algae are in great demand as foods, over seventy varieties being eaten in Hawaii. Algae are rich in carbohydrates, mineral salts, and vitamins. "Irish moss," an alga growing along the coast from North Carolina to Maine, is collected, processed, and, because of its high mucilage content, used in the making of desserts.

The Four Classes of the Algae.—

Blue-green algae	(Myxophyceae)
Green algae	(Chlorophyceae)
Brown algae	(Phaeophyceae)
Red algae	(Rhodophyceae)

The names of the four classes of the Algae are based upon the characteristic differences in color. However, the color differences are not the sole nor yet the most important ones. The members of each class have certain characteristics in common, such as cell structure, reproductive processes, etc., which in general are more dependable as indicators of relationship than is color. There are, in fact, some Myxophyceae which are brown, some Chlorophyceae which are red, and some Phaeophyceae and Rhodophyceae which are green.

THE MYXOPHYCEAE—BLUE-GREEN ALGAE

Characteristics of the Myxophyceae.—The simplest and most primitive green plants belong to this group. The plant body is extremely simple, in fact, in many instances, a single cell or a colony of similar cells. The cells are without definite nuclei and, with few exceptions, without any distinct chloroplasts. The pigments of the cells are generally restricted to the outer region of the protoplast, but this colored part is not sharply marked off from the colorless protoplasm within, which is called the central body. The central body has been called an "incipient nucleus," and may represent a stage in the evolution of a true nucleus. It probably contains in all cases granules of a material similar to the chromatin of the nuclei of most plants. The cell walls of the Myxophyceae consist of a thin,

firm inner layer, chiefly cellulose, and an outer gelatinous layer. In addition to chlorophyll the plants of this group generally contain

FIG. 155. *Synechococcus.* A blue-green alga, the cells of which are solitary except during fission. Several stages of fission are shown as well as a single cell almost ready for division.

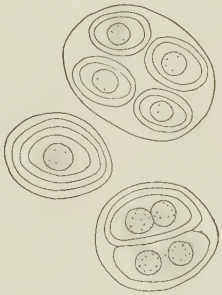


FIG. 156 *Gloeocapsa,* a blue-green alga, the cells of which occur generally in groups, the cells formed by the fission of a single cell being held together by the gelatinous coating of the cell from which they came.

one or more accessory pigments, the commonest of which is a blue pigment called **phycocyanin.** A red accessory pigment is present in some forms, so that there are "blue-green" algae which are red and which may give a bright red color to water when present in large quantities. One such form, *Trichodesmium erythraeum,* is a floating marine plant which gives a bright red color to the water when present in large quantities. The Red Sea owes its name to the occasional coloring of its waters by this organism.

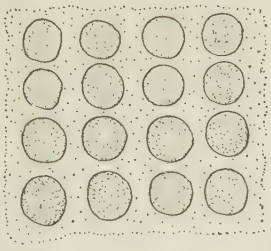


FIG. 157. *Merismopedia,* a blue-green alga, the cells of which are held together by a gelatinous matrix. The cells divide in two planes only and as a result the groups of cells have the form of flat plates. These may grow to considerable size and consist of scores of cells.

Almost all Myxophyceae secrete considerable quantities of a gelatinous substance which forms a sheath or matrix around the cells or cell groups.

The product of photosynthesis in the Myxophyceae is not starch or glucose but another carbohydrate, glycogen, which is also found in many fungi and frequently in animals.

There is **no sexual reproduction** in the Myxophyceae.

Distribution of the Myxophyceae.—These plants are abundant in fresh and in brackish water and in water contaminated by sewage, and many forms are found in the sea. A number of forms are abundant in moist soil, especially when it is rich in organic matter; on trunks and branches of trees; and on rocks. They form the principal vegetation of hot springs, such as those in the Yellowstone National Park, where they have been found living in water as hot as 87° C.

FIG. 158. A portion of a filament of *Oscillatoria,* one of the commonest blue-green algae. The divisions of the cells take place in parallel planes so that the cell groups are filamentous and unbranched. As the result of the death of a cell here and there, the filament breaks up into short pieces called hormogonia.

Representatives of the Myxophyceae.—The simplest members of this group, such as *Synechococcus,* consist of single cells which are generally spherical or oval. These single cells, which constitute the plant body, are capable of carrying on all essential life processes. They generally live either immersed in water or in very moist habitats where they are wet most of the time. Through the surface of the cell the protoplast absorbs water, inorganic salts, and the gases, carbon dioxide and oxygen. By photosynthesis the protoplast forms carbohydrates which, as in the higher plants, are used in part for respiration and in part for the formation of substances from which new protoplasm can be built up.

In some forms, such as *Gloeocapsa,* the daughter cells resulting from fission are held together by a gelatinous matrix in groups of two, four, eight, or more cells, each cell, however, being entirely independent of the other cells of the group.

In other forms, as *Nostoc* and *Oscillatoria,* the cells resulting from a succession of fissions remain attached and form chains or filaments. In *Nostoc,* many hundreds of these filaments are held within a gelatinous mass produced by the cells. Here and there in the *Nostoc* filaments, large, colorless cells, called **heterocysts,** occur. The filaments break apart easily at these heterocysts, forming short filaments

capable of locomotion and known as **hormogonia** (singular, **hormogonium**), which grow into long filaments by growth and division of their cells. Hormogonia are formed in *Oscillatoria* by the death of a cell or group of cells here and there in the filament. The filaments of *Oscillatoria* can move from place to place, exhibiting a swaying or oscillating as well as a twisting or rotating movement.

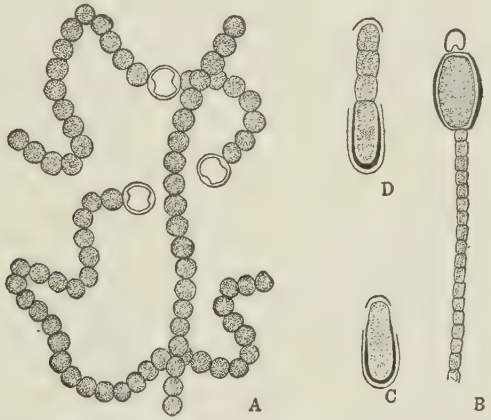


FIG. 159. *A*, *Nostoc*, filament showing heterocysts; *B*, *Cylindrospermum* filament showing heterocyst and thick-walled resting spore; *C* and *D*, germinating resting spores.

Nostoc shows a slight advance over such forms as *Oscillatoria* in the formation of resistant cells, or asexual spores, from some of the ordinary vegetative cells. These spores germinate to form new filaments when conditions become favorable.

Nostoc and *Oscillatoria* are probably to be considered rather as colonies of unicellular plants than as multicellular individuals, although the distinction between these two states is not a very sharp one.

THE CHLOROPHYCEAE—GREEN ALGAE

Characteristics of the Chlorophyceae.—This is the largest of the four groups of algae. All the plants included in this group have chloroplasts and a definite nucleus. These two characteristics distinguish the Chlorophyceae from the blue-green algae but not from the red or brown algae. Most of the green algae possess in their cells only the pigments which are typically present in green cells—chlorophyll *a* and chlorophyll *b*, carotene, and xanthophyll.

The cell walls with few exceptions consist mostly of cellulose. In most of the green algae, starch is the first visible product of photosynthesis, although some produce no starch but have oil as the only visible product of photosynthesis.

Distribution of the Chlorophyceae.—Members of this group are found in every conceivable moist place where the temperature is not very high and where light can penetrate. The larger number are fresh-water plants. Relatively few are marine, and most of these occur in tropical seas. There are a number of green algae which are commonly found in soil, but they can live, of course, only very near the surface. A few green algae, such as the common *Protococcus* and *Trentepohlia,* are epiphytes on the bark of trees or attached to fence posts or other objects.

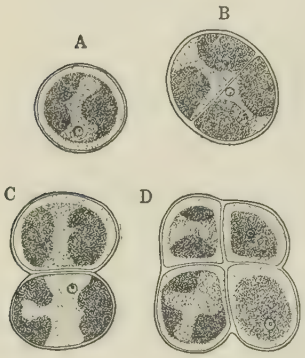


FIG. 160. *Protococcus,* a simple alga, in which the cells remain united for some time after fission, forming groups of varying size and cell number.

A green alga resembling *Protococcus* is the autophytic component of most lichens, growing in symbiosis with a fungus. There are a few simple green algae which are regularly found in the bodies of certain primitive animals such as the sponges. Some actually live within the cells of animals, as does the alga *Chlorella* in the cells which line the body cavity of the hydra (*Hydra viridis*).

Representatives of the Chlorophyceae.—One of the simplest of the green algae is *Protococcus,* probably the commonest, most widely spread green alga in the world. It forms a coating on the shaded and therefore more moist side of the branches and trunks of trees, rocks, and fence posts. It may occur singly, or in groups of two or four individuals. These unicellular plants are entirely independent, carrying on all essential life processes within the single cell. Reproduction is asexual, occurring by fission only, that is, by the division of a single-celled individual into two new unicellular individuals of equal size. These two new individuals, produced by fission, together contain all the material of the single parent cell.

FIG. 161. *Ulothrix zonata*. *A*, portion of a filament showing the holdfast cell at the base, and the ordinary vegetative cells. *B*, a portion of a filament which has formed gametes in three cells (above) and zoospores in four cells (below). The gametes are generally smaller than the zoospores and always bear two cilia each, the zoospores each have four cilia. *C*, a zoospore which has just escaped. *D*, a germinating zoospore. *E*, *F* and *G*, stages in the fusion of gametes. *H*, a zygote in the resting condition. *I*, germinating zygote showing the division of its protoplast into a number of zoospores. (*A-D* after Dodel, *E-H* after Oltmanns.)

A more complex type is *Ulothrix,* an unbranched, filamentous alga, in which the basal cell of the filament is specialized to form a **holdfast.** Here is a simple case of specialization of one cell of a group for a function not performed by other cells of the group. In this we have what seems to be the beginning of the development of the multicellular type of plant as distinct from the strictly unicellular and the colonial type.

Ulothrix reproduces both asexually and sexually. In the former case, the protoplast of some or all of the cells of a filament may contract and round up, each protoplast thus forming from one to eight naked protoplasmic bodies. Each of these is equipped with four extremely slender whip-like filaments of protoplasm, called **cilia,** by means of which the bodies are propelled through the water. These naked, motile, asexual bodies are called **zoospores.** Soon after their formation they escape from the filament by a hole which is formed in the lateral wall, and start to swim around in the water. After a time they attach themselves at the ciliated end to some other alga, to a stone, or to some other object in the water. Subsequently, the cilia are lost and a cell wall is formed, and then by elongation and division the zoospore develops into a new filament. It will be seen that asexual reproduction by spores in *Ulothrix* involves the formation of special, motile masses of protoplasm, known as zoospores, which are able to develop directly into new individuals. *Ulothrix* reproduces sexually by the production of **gametes.** A gamete is a protoplast which, unlike a zoospore, is incapable by itself of developing into a new individual, but must first unite with another gamete. The body formed by the fusion of two gametes is called a **zygote.** In *Ulothrix,* the gametes are small, naked, biciliated masses of protoplasm, and are all alike in size and structure. Such gametes are called **isogametes.** Their fusion in pairs is known as **conjugation,** which results in a heavy-walled resting spore, the **zygospore.**

The development of the gametes in *Ulothrix* is very similar to the process of zoospore formation. The gametes arise from divisions of the protoplasts of the cells of the filament but are generally smaller than the zoospores, a single cell often giving rise to as many as sixteen or thirty-two gametes. Each of the gametes has two cilia instead of the four of the zoospores. The zoospores give rise

to new filaments directly, whereas the protoplast of each zygospore, on germination, divides to form a number of zoospores which then produce new filaments. Zoospores are not resistant to unfavorable conditions, as they are naked protoplasts, but zygospores may be very resistant, owing partly to their heavy walls.

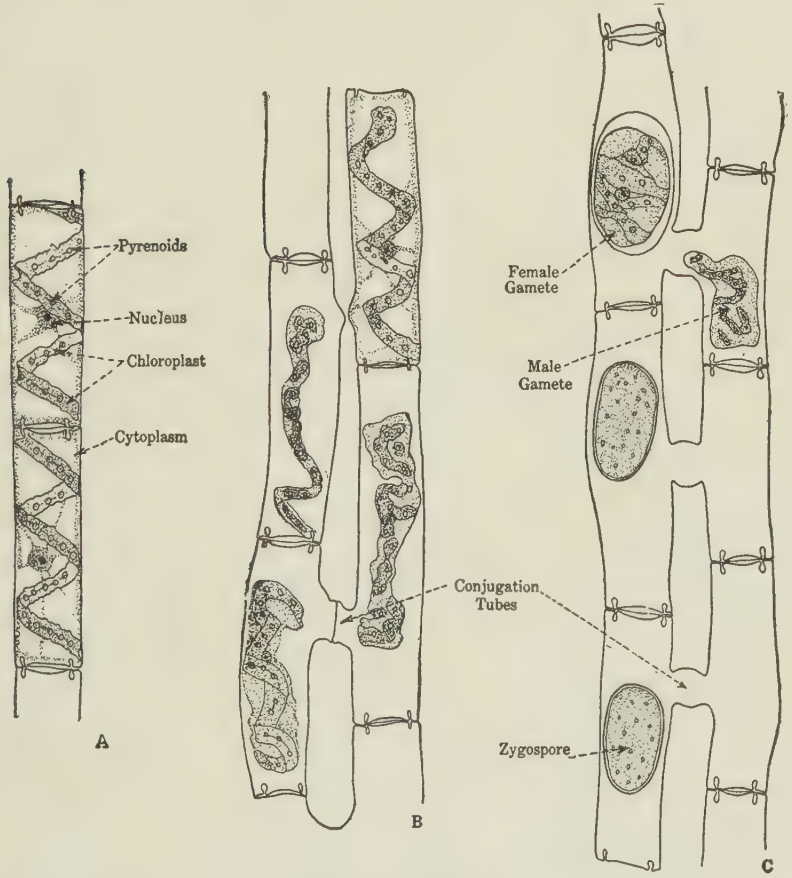


FIG. 162. *Spirogyra.* To the left two cells from a filament in the vegetative condition. The other two figures show successive stages in scalariform conjugation.

Another very common green alga is *Spirogyra,* one of the free-floating algae known as "pond scum." The filaments of *Spirogyra* are surrounded by a layer of mucilage which can sometimes be seen under favorable illumination and which gives a characteristic slimy feel to the plant by which it and closely related forms can be easily

recognized in the field. The most characteristic feature of *Spirogyra* is the spirally arranged ribbon-like chloroplast.

The *Spirogyra* cell is cylindrical in form and is lined by a thin layer of cytoplasm in which the chloroplast or chloroplasts are embedded. The nucleus with the cytoplasm which surrounds it is suspended in the center of the single large vacuole, either by fine strands of cytoplasm or by a narrow band of cytoplasm.

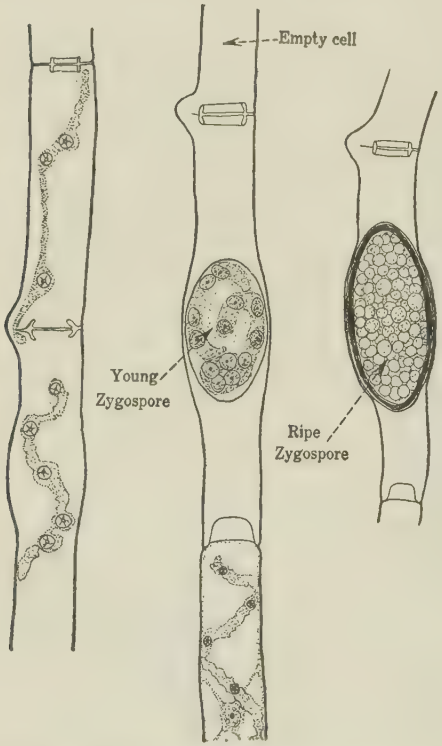


FIG. 163. *Spirogyra*, showing three stages in lateral conjugation.

No zoospores or other nonsexual spores are produced by *Spirogyra*. The gametes are the protoplasts of ordinary vegetative cells. Usually, conjugation takes place between the cells of two different filaments, but it may take place also between adjacent cells of the same filament. In the former type of conjugation, tubular outgrowths are produced on the adjacent sides of the cells of filaments which are in contact with each other. The outgrowths from cells which lie opposite one another in the two filaments become attached at the ends, and as these outgrowths elongate the filaments are pushed apart. Finally the walls separating the extensions of the conjugating cells are dissolved away, and the cell cavities then communicate with each other through the conjugating tubes. Meanwhile, the protoplasts which are to fuse contract somewhat. Then the protoplasts (gametes) from one filament pass over into the cells of the other filament and fusion takes place. Though the gametes are morphologically alike and therefore are considered isogametes, the fact that those in one filament remain passive whereas those in

the other are capable of movement indicates a slight physiological differentiation of gametes.

When all the cells of two filaments conjugate, one filament becomes empty and every cell of the other filament contains a

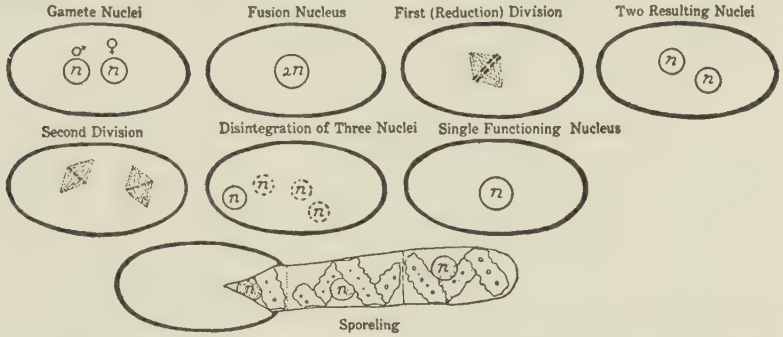


FIG. 164. Diagrams showing nuclear changes in the zygospore of *Spirogyra* from conjugation to germination.

zygote, unless the cells of one filament are shorter than those of the other. In either case the zygote forms a thick wall which

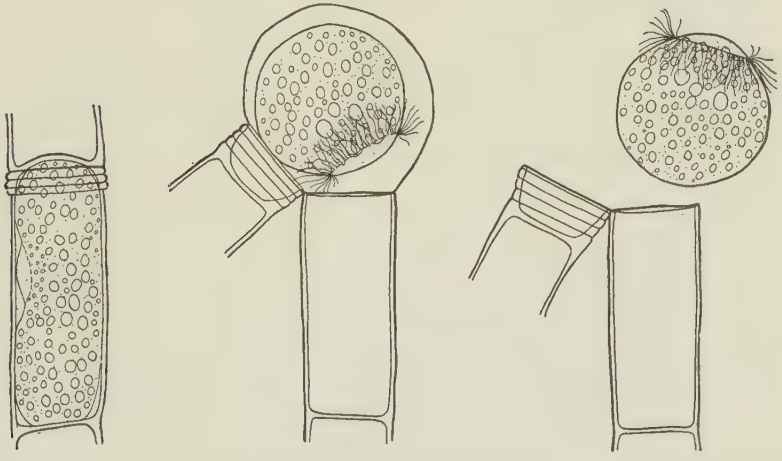


FIG. 165. Formation and escape of a zoospore in a species of *Oedogonium*. (Redrawn from Hirn.)

consists of three layers. The zygospore is highly resistant to extreme cold and to drought. It generally sinks to the bottom of

the pond or stream where it is formed and, after a period of rest, germinates. Germination is dependent upon conditions favorable for the vegetative activities of *Spirogyra,* that is, abundance of water, moderate temperature, and sufficient illumination. When the zygospore germinates, it absorbs water, and the protoplast

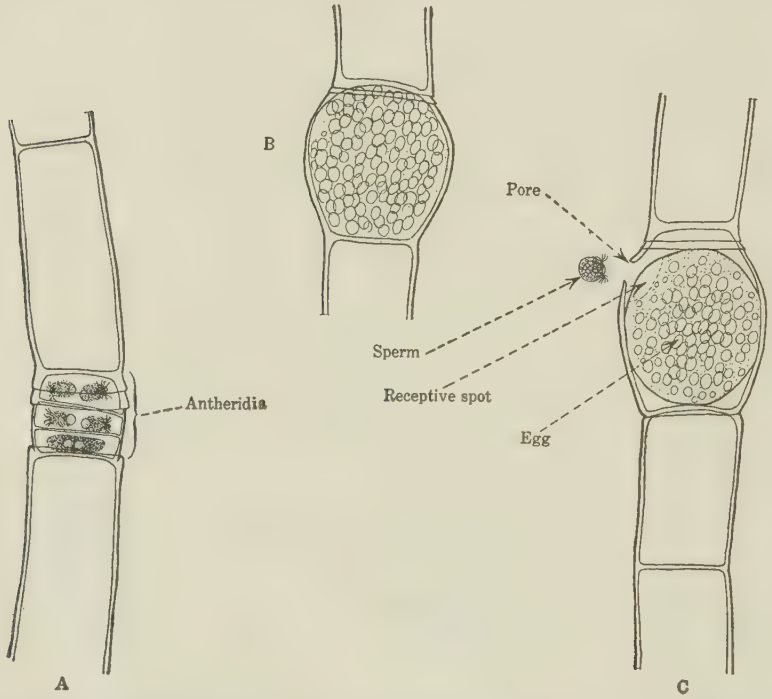


Fig. 166.—*Oedogonium. A,* portion of a male filament showing several antheridia. *B,* an immature oogonium. *C,* part of a female filament showing a ripe oogonium, the egg cell of which is about to be fertilized. For the ripe oospore and the structure of a vegetative cell, see Fig. 167*A*. *C* is somewhat diagrammatic.

within increases in size and bursts the outer and middle wall of the spore; the inner cellulose wall becomes extended as the protoplast pushes out. The protoplast of the germinating zygospore forms a tube which elongates and develops into a new filament.

Oedogonium is a common green alga showing a greater degree of differentiation than any form thus far mentioned. It reproduces by means of zoospores and also by **heterogametes,** which are gametes differing in size, behavior, and amount of food reserve. In

plants which produce heterogametes the zygote is formed by the fusion of a male gamete, or sperm, with a female gamete, or egg cell, and never by fusion of two gametes of the same sort. The process of fusion of heterogametes is called **fertilization**, and the resulting zygote an **oospore.**

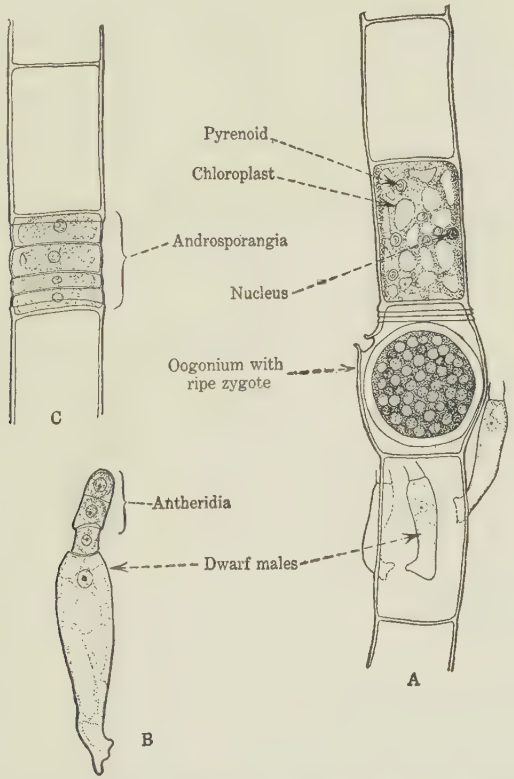


FIG. 167. A species of *Oedogonium* which produces dwarf males. *A*, portion of an oogonial filament showing the structure of a vegetative cell, an oogonium containing a ripe zygote and three dwarf males which have discharged their sperms. *B*, a single dwarf male showing the holdfast cell at the base and the antheridia. *C*, a portion of a filament with androsporangia within which are developing androspores (zoospores which germinate and give rise to dwarf males.)

The basal cell of the filament forms an organ of attachment, or holdfast. Not all the cells in the filament are able to divide and thus add to the length of the filament; certain cells alone have this power. Gametes are not produced in ordinary vegetative cells, as in *Ulothrix* and *Spirogyra,* but in special organs called

gametangia, much different in form from the vegetative cells, though developed from them. On account of this considerable physiological division of labor, *Oedogonium* is certainly to be considered a multicellular plant.

In most species of *Oedogonium* each zoospore consists of the entire protoplast of a vegetative cell. The zoospores are provided with a ring or collar of cilia around the colorless forward end. Generally only a few cells of a filament produce these motile spores.

The male gametes, or sperms, of *Oedogonium* are produced in short cylindrical cells, which are known as **antheridia** or **male gametangia**; the sperms are much smaller than the female gametes, or eggs. The sperms are like miniature zoospores in form, and are produced in the same or in different filaments, and in much larger numbers than the egg cells. The female gametes, or eggs, are produced in spherical or oval cells, known as **oogonia** or **female gametangia**. Eggs are without cilia and remain within the oogonium until after fertilization. After the development of the egg a pore is formed, through which the sperm may enter, by the dissolution of a small area of the oogonium wall. Almost immediately after the entrance of the sperm into the egg, a thick wall is formed about the zygote. Decay of the oogonium wall releases the oospore, which is resistant to the conditions unfavorable to the vegetative cells, as are the zygospores of *Ulothrix* and *Spirogyra*. The oospore does not produce a new plant directly, but its protoplast divides to form four zoospores which in turn give rise to the new filaments. The striking similarity between the sperms and zoospores distinctly indicates the possibility of the origin of gametes from zoospores.

Systematic botanists have divided the Chlorophyceae into a number of smaller groups, each of which seems to have evolved independently from some ancestors belonging to a single group of simple organisms, probably the flagellates. Within several of these smaller groups it is possible to find series of genera which indicate the development from very simple forms without sexual reproduction, through forms of more complexity and with isogamous sexual reproduction (by means of similar gametes), to heterogamous, larger and still more complex forms in which the gametes are distinctly differentiated. It appears that among these plants there has been, at least in several of the smaller groups, a parallel development

from very simple to more complex plant bodies, and that sexual reproduction and the development of heterogamy (reproduction by unlike gametes) have taken place independently in each of these different groups.

Each zygospore, of such forms as *Spirogyra,* and each oospore, of such heterogamous plants as *Oedogonium*, contain chromatin derived from the male and female gametes, and thus have twice as many chromosomes as the nuclei of the vegetative cells. In all plants having sexual reproduction there is such a doubling of the chromosome number when the zygote is formed. At some stage in the life history of such plants, there is necessarily a reduction in the number of chromosomes from the $2n$ or diploid number to the n or haploid number. This reduction division takes place at different points in the life history of different plants. In *Spirogyra,* for example, the nucleus of the zygospore very promptly undergoes division and the resulting daughter nuclei again divide so that the zygote has four nuclei. Three of these soon disintegrate. One of the two nuclear divisions is a reduction division, in which the chromosome number is reduced to the normal number for ordinary cells of the species. In *Oedogonium,* four zoospores are developed from each oospore, and one of the two divisions which results in the formation of these four zoospores is a reduction division, so that the resulting nuclei have half the number of chromosomes which appear at the first division of the zygote nucleus.

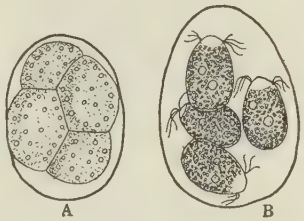


FIG. 168. Germination of oospore of *Oedogonium*. *A*, the protoplast of the zygote which has divided into four protoplasts. *B*, the four zoospores formed from the four protoplasts. The oospore has a nucleus with "$2n$" chromosomes, the zoospores having nuclei with "n" chromosomes.

THE PHAEOPHYCEAE—BROWN ALGAE

Characteristics of the Phaeophyceae.—The third class of the algae, the brown algae or Phaeophyceae, includes the largest and the most highly differentiated of the thallophytes as well as some forms of small size and very simple structure. The range of size is from species which are microscopic to such genera as *Macrocystis,*

which may attain a length of several hundred feet. No unicellular organisms are found in this group. All the Phaeophyceae have cells with definite nuclei and distinct plastids. These latter contain, in addition to chlorophyll *a*, chlorophyll *b*, carotene, and xanthophyll, a

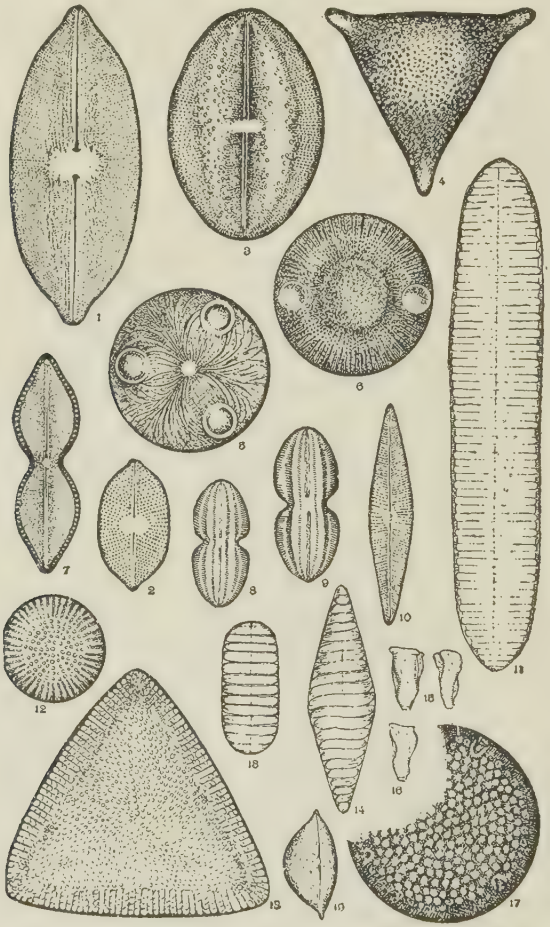


FIG. 169. Diatoms (all highly magnified) showing various forms and markings. (From Wolle's *Diatomaceae of North America.*)

brown accessory pigment, called **fucoxanthin**, which usually entirely hides the green color of the chlorophyll. All the brown algae normally grow attached, but plants may become detached and still survive.

Off the southeast coast of the United States is a great area, about a quarter of a million square miles in extent, of floating seaweed called the Sargasso Sea. The principal plants found there are two species of *Sargassum,* a plant belonging to the brown algae. Pieces of these plants probably were brought by ocean currents from the coasts of the West Indies or of tropical America where they

FIG. 170. Structure and reproduction of a species of *Ectocarpus*. *A*, habit drawing. *B*, portion of a plant showing sporangia. *C*, a single gametangium and vegetative cells. *D*, portion of a plant showing gametangia. *E*, two zoospores. *F*, several stages in conjugation, including a zygote, to the right of the letter. *G*, two gametes about to conjugate. (*A-D* after Setchell and Gardner.)

had broken off from plants growing attached there. For ages they have multiplied vegetatively in the Sargasso Sea.

In the Phaeophyceae no resting spores are produced, and all motile cells, whether zoospores or gametes, have two cilia which are laterally attached.

Distribution of the Phaeophyceae.—These plants are much more common and better developed in the cool ocean waters of the

temperate zones than in warm tropical seas. Only a few species are found growing in fresh water.

Representatives of the Phaeophyceae.—*Ectocarpus* is a form which, like *Ulothrix,* illustrates the probable origin of sexual reproduction. The gametes are similar to zoospores in structure but normally do not develop new plants without fusion to form a zygo-

FIG. 171. A large kelp (*Pelagophycus*) from the Californian coast. (Photograph furnished by W. A. Setchell.)

spore. Among the different species of *Ectocarpus* there are apparently the beginnings of a differentiation of gametes. In some forms there is a slight difference in size, and it is said that in such cases only gametes differing in size are able to fuse. In some other species, in addition to size differences, there is also said to be a difference in degree of motility, the larger gametes moving less actively and coming to rest earlier than the smaller ones which fuse with them as they become quiescent. In short, in the genus *Ectocarpus* as a whole, little distinction seems to exist between zoospores and gametes, and there occur various gradations between isogametes and heterogametes.

The kelps include those plants which form the extensive beds of large brown seaweeds off the Pacific Coast. They possess a holdfast, or organ of attachment which superficially resembles a root system, a stalk or stipe, and expanded blade-like portions which in their form suggest the leaves of the seed plants. There is also a consider-

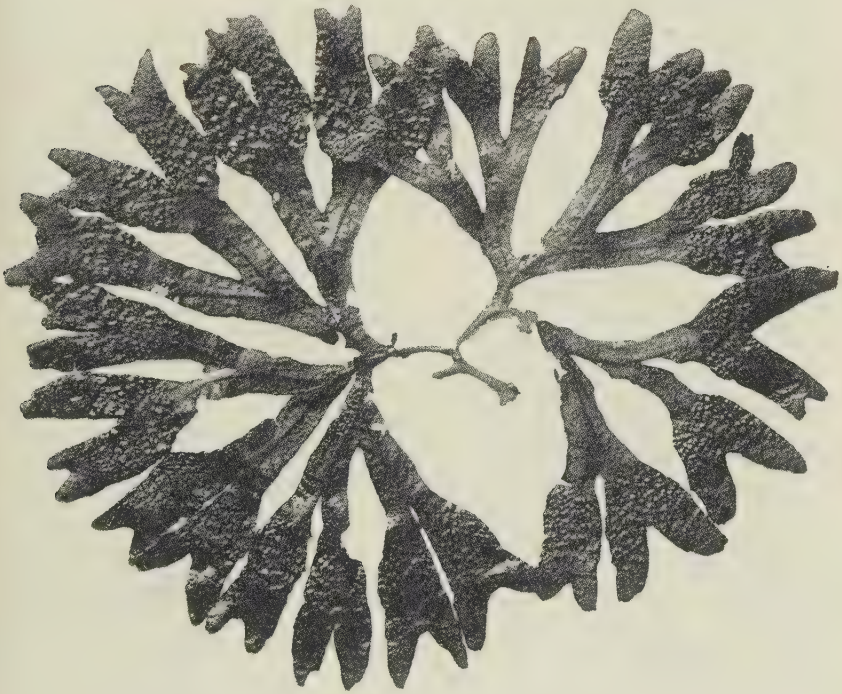


FIG. 172. A frond of a species of *Fucus*, showing the dichotomous method of branching, and the fruiting branches with numerous conspicuous swellings (openings of the conceptacles). (Photograph furnished by Gardner and Setchell.)

able differentiation of tissues, but anatomically they are not at all like leaves.

In the kelps is found a condition known as *alternation of generations*, which also exists in certain Rhodophyceae and which is the rule in all the Bryophyta, Pteridophyta, and Spermatophyta. The zoospores which are formed give rise, upon germination, to very small plants quite unlike the typical kelp plants on which the zoospores were produced. These minute plants are of two sorts, antheridial and oogonial, producing respectively sperms and eggs. The sperms

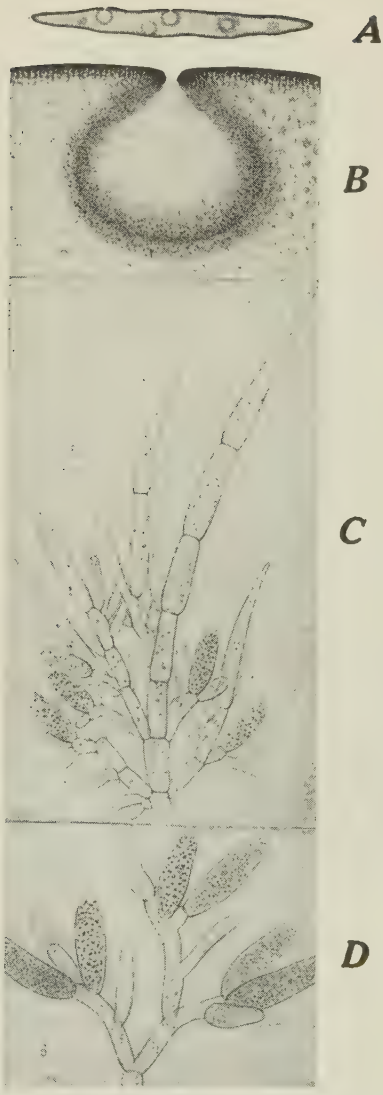


FIG. 173. A dioecious species of *Fucus*. *A*, Cross section of a fruiting tip of a male plant, showing the compact outer region (the cortex), the loose tissue within (the medulla), and several antheridial conceptacles. *B*, a single antheridial conceptacle in section showing the opening to the surface (the ostiole) and the antheridia-bearing hairs which arise from the inner surface. *C* and *D*, antheridia and the branched hairs upon which they are borne (After Thuret.)

FIG. 174. A dioecious species of *Fucus*. *A*, a cross section through a fruiting branch of a female plant showing the cortex, medulla, and several oogonial conceptacles. *B*, a single oogonial conceptacle in section, showing the ostiole and the oogonia and paraphyses which line the conceptacle. *C*, a portion of the floor of the conceptacle showing an oogonium attached by its stalk cell and surrounded by a number of paraphyses. Note that the protoplasm of the oogonium has undergone cleavage to form the eight eggs which have not yet rounded up. (After Thuret.)

and eggs fuse forming zygotes, which, on germination, develop into typical kelp plants. Thus there are two generations or phases in the life cycle, (1) a gamete-producing generation (**gametophyte phase**), the nuclei of all the cells of which, including the gametes, have the haploid chromosome number, and (2) a generation (**sporophyte phase**) with diploid nuclei giving rise to asexual zoospores whose nuclei as the result of a reduction division have the haploid chromosome number.

Fucus is a brown alga which also shows considerable complexity of the plant body and much differentiation of tissues as compared with the blue-green and green algae. There is a distinct differentiation of gametes, the sperms being very small in size, highly motile,

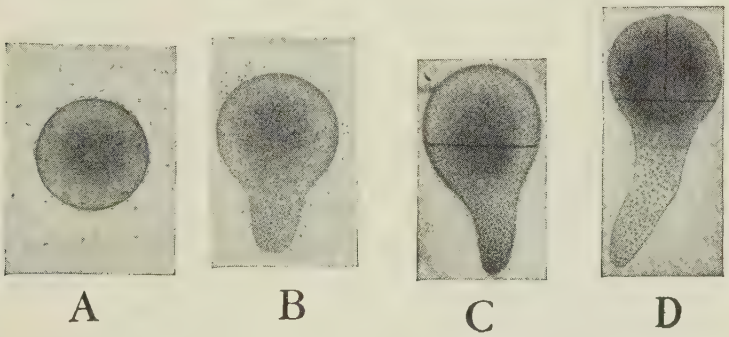


FIG. 175. Fertilization of the egg and germination of the oospore of a species of *Fucus*. *A*, an egg surrounded by many sperms. *B*, an oospore germinating. The tubular outgrowth, which later forms a holdfast at the tip, arises always on the side of the oospore away from the light. *C*, the young plant has divided into two cells by a transverse wall. *D*, a wall at right angles to the first divides the upper of the cells into two cells. (After Thuret.)

and produced in very great numbers, whereas the eggs are large (the volume may be as much as thirty thousand times as great as that of a sperm), relatively few in number, and without power of locomotion. The eggs are expelled from the oogonia, and fertilization occurs outside in the sea water. The resulting zygote does not produce a thick wall and becomes a resting spore, but germinates at once to produce a new plant like the one which bore the gametes which gave rise to it.

In *Fucus*, the reduction of chromosomes, from the double or diploid number characteristic of "the plant" to the half or haploid number found in the egg and sperm, takes place at the first division of the antheridial and the oogonial cells, that is, not long before the

time of gamete formation. At fertilization the chromosome number is doubled, so that the oospore and the plant into which it develops have nuclei with the diploid chromosome number.

THE RHODOPHYCEAE—RED ALGAE

Characteristics of the Rhodophyceae.—The fourth class of the algae is made up of plants which are mostly marine, although a few species live in fresh water. All members of this class are multicellular. In general they are clearly more differentiated than the green algae, but as a group are characterized by simpler structure than the kelps and *Fucus*. Most of the vegetative cells have a single nucleus, and the plastids, which may occur in large numbers in each cell, contain, in addition to chlorophyll *a*, chlorophyll *b*, carotene, and xanthophyll, an accessory pigmen called phycoerythrin. True starch is never found in the Rhodophyceae, but grains of a reserve carbohydrate, which stains red instead of blue when treated with iodine, are often present.

FIG. 176. A portion of a red alga, *Pterosiphonia*, a genus closely related to *Polysiphonia*. (Photograph furnished by N. L. Gardner.)

In many red algae the cell walls are very thick, so that the protoplasts appear to be embedded in an extensive gelatinous matrix. Some of these plants, which have a finely branched plant body, are certainly to be considered the most delicate and beautiful of all marine plants. In one group of red algae, the coralline algae, the cell walls become encrusted with large quantities of carbonate of lime and are strongly suggestive of corals.

No ciliated cells have been found in the red algae. Sexual reproduction is always heterogamous, and the life history of these plants is usually rather complicated, involv-

ing in many species an alternation of asexual (diploid) and sexual (haploid) generations.

Distribution.—The Rhodophyceae are abundant in the temperate seas, but the number and variety of forms are greater in the warmer tropical and sub-tropical waters. They are generally found below lowtide level and may grow at depths as great as 650 feet.

SUMMARY

In the Algae, various steps in the evolution of the plant body and the development of sex are exemplified. The simpler algae are unicellular plants, each separate cell, which constitutes the plant body, being capable of carrying on all the necessary processes and of existing solitary or in groups without any constant form. A somewhat more advanced condition is one in which the cells, each of which is still capable of carrying on all the essential life processes, are united into groups of a definite and constant form. Such groups of unicellular plants are called colonies. A further step in the evolution of the plant body is that by which certain cells of a relatively simple group are specialized to perform some function for the whole group. For example, in such a plant as *Oedogonium,* there are cells specialized as holdfast cells and others specialized for reproduction. There is still greater specialization of parts and tissues in such algae as *Fucus* and the kelps.

In the most primitive algae, reproduction is by fission. When the cells of such plants are united in colonies, the colonies may break up into groups of a few cells (hormogonia production in *Oscillatoria*), each group growing by the fission of its different cells until larger colonies are again formed. Such plants may produce resistant spores (thick-walled cells with much reserve food) which can carry the organism over periods of drought or unfavorable temperature.

In several groups of algae, zoospores (motile, asexual spores) were probably produced before sexual reproduction originated. The zoospores serve for multiplication and for wider distribution of the species. They appear to have been the structures from which gametes originated in the evolution of sexual reproduction in plants. Probably sex developed independently in several different groups of algae, perhaps as the result of accidental fusion of zoospores.

In the more primitive groups of algae having sexual reproduction, the gametes are alike in structure (isogametes). In less primitive forms they are structurally of two kinds (heterogametes, i.e., sperms and eggs).

In some of the forms which produce both zoospores and gametes, as in *Oedogonium,* the male gametes are essentially the same in structure as the zoospores, though smaller in size.

In several distinct algal groups, there are slight differences in the size of the gametes of a given species, or in the duration or degree of their motility. Such species exhibit the beginnings of differentiation of the sex cells into male and female gametes.

In forms in which the gametes are further differentiated there may exist great differences in the size of the two kinds, complete loss of motility of the female gamete, and great increase in the number of male gametes produced by a single plant, together with corresponding decrease in the number of female gametes. In some of the algae in which there is a very marked differentiation of the gametes, the female gamete is retained within the gametangium (oogonium) until after fertilization. Thus, sex probably originated in the plant kingdom merely as a modification of an asexual method of reproduction; and once sex originated, it must have had some advantage for the plant, for in spite of the simplicity of asexual reproduction, sexually reproducing plants have gone a long way towards "inheriting the earth."

The following summary of methods of reproduction in the Thallophyta indicates the spore types involved:

Asexual reproduction (without union of protoplasts):

(*a*) Fission—division of a single-celled individual into two new individuals of equal size (Fig. 155).

(*b*) Asexual spore formation—motile asexual spores or zoospores (Figs. 161 *C* and 164) and non-motile asexual spores (Figs. 159 and 188).

Sexual reproduction (with union of protoplasts):

(*a*) Conjugation—the fusion of similar gametes (isogametes) to form a zygospore (Figs. 161 *E* and 162).

(*b*) Fertilization—the fusion of dissimilar gametes (heterogametes) to form an oospore (Figs. 165 and 191).

CHAPTER XI

THALLOPHYTA
FUNGI

(THALLOPHYTA WHICH DO NOT MAKE THEIR OWN FOOD)

THE fungi are a group of plants of great economic importance. Bacteria, yeasts, molds, mildews, rusts, smuts, mushrooms—these are a few representatives, mere mention of which indicates at once the significance of this assemblage of plants.

The fungi do not constitute a natural group. Among them are included plants which are certainly more distantly related to each other than they are to certain plants outside the fungi. The single definite basis of distinction between the algae and the fungi is the fact that the algae can make their own food from simple inorganic food material, that is, they are **autophytic**, whereas the fungi, lacking chlorophyll, must secure their food ready made from some other living organism or from the dead remains or products of some organism, that is, they are **heterophytic.**

An organism deriving its food from the living body of either a plant or animal is called a **parasite.** An organism obtaining its food from the dead body or the non-living products of another plant or animal is called a **saprophyte.** Plant pathologists are primarily concerned with parasitic fungi, for these are the organisms that attack many useful plants, derive nourishment from them, and induce injuries which we speak of as due to plant diseases. The losses caused by plant diseases are immense.

Plant diseases have had a marked influence on human life. Throughout modern history are many records of the ravages due to plant diseases. Ergot poisoning, caused by *Claviceps purpurea*, a fungus which infests rye and is evidenced by the curved blue to black, hard sclerotia in rye heads, has occurred as an epidemic many times in the history of European countries. In 1845, approximately 80 per cent of the potato crop of Europe was destroyed by late blight of potatoes caused by a phycomycete (*Phytophthora infestans*). That year, in Ireland, where the potato was the chief food crop, the loss was almost 100 per cent, and a famine resulted. The epidemic initiated an emigration from

Ireland that lasted for fifty years. Recently, by crossing certain desirable commercial potatoes with a wild potato species from tropical America, varieties have been found which are highly resistant to this disease. In 1851, powdery mildew of grape caused by *Uncinula necator* threatened the wine industry of southern Europe. Again, in 1878, the wine industry of that country was menaced by the ravages of another downy mildew (*Plasmopara viticola*). Peach yellows, a virus disease, actually eliminated the peach industry in certain sections of Maryland, Delaware, and Michigan from 1890 to 1900. Curly top of sugar beets, another virus disease, has caused serious damage to the crop in western states, in many instances closing sugar factories. The development of resistant varieties has saved the sugar-beet industry in many districts. Chestnut blight or chestnut bark disease, caused by *Endothia parasitica*, has swept through the Appalachian region, in places causing 75 per cent destruction. Only a few examples have been cited above to show the importance of plant diseases in human affairs. It has been estimated that the average annual loss in the United States from diseases caused by bacteria and other fungi in the ten leading crops, during the eight-year period 1919 to 1926, inclusive, amounted to more than $780,000,000.

Diseases of plants are not all of parasitic origin. Diseases due to adverse environmental conditions, such as deficiency or excess of water, or of mineral salts, or temperature, are clearly of non-parasitic origin.

Symptoms of disease are varied. There may be a blight of leaves, a damping-off of seedlings, rot, canker, leaf spot, wilt, chlorosis, etc.

The control or eradication of plant diseases is attempted in various ways: crop rotation, sanitation, soil sterilization, spraying and dusting, seed treatment, eradication of alternate hosts, quarantine, and disease resistance. In recent years great progress has been made in the breeding of strains of crops and ornamental plants that are wholly or partially immune to specific diseases. Thus have the plant breeder and plant pathologist cooperated in reducing the losses due to plant diseases.

In the condition called parasitism, one organism, the parasite, secures its food entirely or in part from the tissue of another organism. The organism at the expense of which the parasite lives is called the **host**. The parasite contributes nothing to the advantage of the host.

We shall consider the fungi as consisting of the following five groups:

Class 1.—The Schizomycetes or Bacteria (Fission Fungi).
Class 2.—The Myxomycetes (Slime Fungi).
Class 3.—The Phycomycetes (Algal Fungi).
Class 4.—The Ascomycetes (Ascus Fungi).
Class 5.—The Basidiomycetes (Basidium Fungi).

There are a considerable number of fungi of great economic importance whose complete life histories have not been worked out. Because of this incompleteness, they have been placed in no one of the groups given above but in an artificial group called Fungi Imperfecti. The life histories of many fungi, temporarily placed in Fungi Imperfecti, have been worked out, and accordingly such have been properly classified and placed in any one of the three groups, Phycomycetes, Ascomycetes, or Basidiomycetes. At present there are about 24,000 species of fungi referred to the Fungi Imperfecti, among which are those which cause leaf spot of beets, anthracnose of beans, early blight of potatoes, and also "athlete's foot" in man.

BACTERIA

These tiny organisms are all about us. They are found floating in the atmosphere, mostly as "passengers" on dust particles, up to a height of several thousand feet. They are abundant upon the surface of the human body and are present in large numbers in the intestinal tract and on all the mucous membranes. Bacteria are found in soil down to a depth of six feet and more, many millions often being present in a gram of soil. They are, of course, particularly abundant in sewage. Living bacteria are present on the surface of all objects about us except those which have recently been heated to a high temperature or otherwise sterilized. They are seldom found within the tissues of plants and animals except when the organisms are suffering from one of the numerous diseases which bacteria may cause.

Great as is the loss of life and property and the suffering for which some bacteria are responsible, the beneficial effects of bacteria doubtless outweigh the harm they do. Their greatest single service is no doubt the part they play, together with the yeasts and molds, in causing the decay of the dead bodies of plants and animals. Through this process, the carbon, oxygen, hydrogen, nitrogen, sulphur, and phosphorus which make up the bodies of animals and plants, and their products, are reduced to simple compounds, such as carbon dioxide, water, nitrates, sulphates, and phosphates, which can again be used as raw material in food building by living plants. Were it not for this process of decay, in which bacteria play so important a part, much of the available supply of certain essential elements would remain permanently "locked up" in the dead bodies of organisms, so that what remained would not be sufficient for the growth and development of living plants and animals.

The fertility of agricultural soils is largely dependent upon the presence of soil bacteria, which not only make available certain of the essential elements already in the soil, but also may even increase the fertility of the soil by adding to the amount of nitrogen present in it. Bacteria are also essential to various industrial processes of great importance, such as butter and cheese making, and the preparation of vinegar.

Bacteria are the causative agents in a large number of human diseases, including diphtheria, tuberculosis, anthrax, meningitis, typhoid fever, and many others. Most of the serious diseases of domestic animals are also bacterial. Whereas relatively few of the diseases of man and of animals are caused by any fungi except the bacteria, most of the diseases of plants are caused by higher fungi and relatively few by bacteria. Among the few bacterial diseases of plants may be mentioned the following: fire blight of apples, pears, and quinces, crown gall, and black rot of crucifers.

Bacteria are also a source of serious loss to man because of the spoiling of food which is due to bacteria and certain other fungi.

In addition to the soil bacteria which increase the fertility of agricultural soils, there are some, the denitrifying bacteria, which injure the soil by causing the loss of part of its combined nitrogen.

General Characteristics.—The bacteria are strictly unicellular organisms. Sometimes the individuals remain more or less united by a gelatinous matrix, and thus form irregular masses or filaments, but in such cases each cell is self-sufficient and there is no evidence of division of labor among such cells. Bacterial cells, like the cells of the Myxophyceae, are without definite nuclei.

These organisms are very small, but they vary in size within rather wide limits. Among the smallest known bacteria is a rod-shaped form which is $\frac{1}{2}$ micron long and $\frac{1}{5}$ micron wide, but the average dimensions of the rod-shaped forms are probably about 2 microns by $\frac{1}{2}$ micron. (A micron, the unit of microscopic measurement, is 1/1000 of a millimeter or about 1/25,000 of an inch.)

There are three principal morphological types of bacteria: spheres, rods, and spirals. These are spoken of respectively as **cocci** (singular, **coccus**), **bacilli** (singular, **bacillus**), and **spirilla** (singular, **spirillum**).

Some bacteria are able to swim about in a liquid medium by

means of cilia (singular, cilium) or flagella (singular, flagellum). These may arise from various parts of the surface of the cell.

The cell wall differs from that of typical plants in that it contains no cellulose. It is very similar chemically to the protoplasm itself. The protoplast consists of cytoplasm through which are scattered particles of chromatin. That the protoplast is bounded by a semipermeable membrane seems to be clear from the fact that the bacterial cell may be plasmolyzed. This fact is the basis of the commonly used methods of preserving food from spoiling by the use of

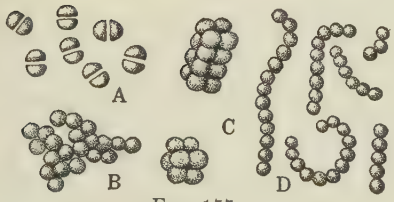


FIG. 177.

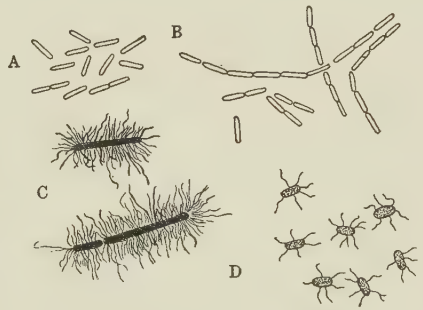


FIG. 178.

FIG. 177. Coccus forms of bacteria. *A, Diplococcus. B, Staphylococcus. C, Sarcina. D, Streptococcus.*

FIG. 178. Bacillus forms of bacteria. *A, Bacillus sporogenes. B, Bacillus subtilis* (young stage). *C, Bacillus proteus. D, Bacillus typhosus.* All magnified about 750×.

salt or sugar, for when foods are preserved in sugar, sugar syrup, dry salt, or brine, the bacteria are unable to grow because of the withdrawal of most of their water by osmosis.

Multiplication of Bacteria.—A bacterium which is abundantly supplied with food and surrounded by favorable conditions will grow to a certain maximum size and then divide by fission into two bacteria of equal size. Under favorable conditions the organisms increase in number by this method very rapidly, so that the descendants of a single bacterium may be, within a few hours, literally countless. Some bacteria may divide as often as once in twenty minutes. It has been estimated that if the cholera organism maintained its maximum rate of fission for twenty-four hours, the bacteria which would thus be produced from one bacterium would number 1,600,000,000,000,000 and would weigh almost half a million pounds.

Spore Formation.—Some bacteria are capable of producing resistant spores. These structures can withstand high temperatures, the presence of poisonous substances, and other unfavorable conditions which are fatal to the ordinary vegetative cell. Fortunately, only a few disease-producing bacteria form spores. With few exceptions, the spores are produced singly within the ordinary bacterial cells. When these spores are formed the protoplast contracts, probably as the result of loss of water, and becomes surrounded by a relatively thick wall. Generally the wall of the cell within which the spore is formed is later dissolved away and thus the spore is freed. When temperature, moisture, food supply, and other conditions are favorable, the spores germinate, each giving rise to a single bacterium.

Since but one spore is produced within a vegetative cell and since each spore gives rise upon germination to a single bacterium, it is evident that spore formation is not a method of multiplication. The spores serve rather as resistant structures able to tide the plant over periods which are unfavorable to vegetative activities.

Fermentation.—Under the general term **fermentation,** we shall include all those chemical changes involved in the breaking down, by bacteria and by other fungi, of the proteins, carbohydrates, and fats of the bodies of plants and animals or of their products. The various bacteria of fermentation accomplish their characteristic chemical changes by the action of enzymes which they produce.

Different groups of bacteria are responsible for the fermentation of each of the three classes of foods, and no doubt often for different substances in each class. The bacteria concerned secure food for their own bodies from the substances fermented, and, from the decomposition of these fermented substances, the energy which they need for their own life processes.

Protein Fermentation.—The term decay is generally applied to the fermentation of proteins when it takes place in the presence of oxygen and when it is therefore not attended by offensive odors. When protein fermentation goes on under anaerobic conditions (in the absence of an abundant supply of oxygen), substances of offensive odor are produced and the process is spoken of as putrefaction. The products of protein fermentation, such as amino acids, may be further broken down by still other bacteria into such very simple

substances as ammonia, nitrogen gas, hydrogen gas, carbon dioxide, hydrogen sulphide, methane (marsh gas), and water.

Fat Fermentation.—Relatively few bacterial forms are capable of fermenting fats, but a considerable number of other fungi may carry on this process.

Carbohydrate Fermentation.—The processes of carbohydrate fermentation are of great economic importance, one of the most important being alcoholic fermentation. Only a few bacteria are able to carry on this process, the most important agents being the yeasts, which are commonly classified among the Ascomycetes. By this process, glucose and similar sugars are transformed into ethyl alcohol and carbon dioxide.

$$\underset{\text{(glucose)}}{C_6H_{12}O_6} = \underset{\text{(ethyl alcohol)}}{2C_2H_5OH} + \underset{\text{(carbon dioxide)}}{2CO_2}$$

After alcoholic fermentation has progressed to a certain point, the concentration of alcohol becomes sufficient to kill off the yeasts or at least to prevent their further activity. Then other (acid) bacteria, which were already present or which enter from the outside, increase rapidly in number and bring about acetic acid fermentation. In this process the alcohol is converted into acetic acid and water.

$$\underset{\text{(alcohol)}}{C_2H_5OH} + \underset{\text{(oxygen)}}{O_2} = \underset{\text{(acetic acid)}}{CH_3COOH} + \underset{\text{(water)}}{H_2O}$$

Another type of carbohydrate fermentation carried on principally by bacteria is lactic acid fermentation, in which milk sugar (lactose) is changed into lactic acid. This occurs in the souring of milk.

Bacteria in Relation to Soil Fertility.—Of the essential elements secured by the green plant from the soil, nitrogen is, next to hydrogen and oxygen, the one which is needed in largest quantities. This element makes up a large part of the molecule of the different proteins of which protoplasm largely consists. Large quantities of the nitrogen from the soil which has been built into plant proteins of crop plants are removed from the field in the grain or other useful parts. Although the waste products from domestic animals, containing much of the nitrogen of the food which they have eaten and utilized in their metabolism, are in

part returned to the soil as fertilizer, much of the nitrogen of the crops removed from the soil is never returned to it. Maintenance of the supply of soil nitrogen is one of the principal problems of soil fertility.

Nitrogen Fixation.—In the absence of all nitrogen except free nitrogen (nitrogen not combined with other elements) the higher plants do not thrive. Nitrogen in the form of nitrates (salts in which nitrogen and oxygen, in the proportion of one atom to three, are united with some metal, as in $NaNO_3$, KNO_3, and $Ca(NO_3)_2$) is the most favorable for the use of crop plants. Nitrogen in the form of ammonium salts, such as ammonium carbonate, $(NH_4)_2CO_3$, can also be used but is less favorable. A number of agencies can cause the free or gaseous nitrogen of the atmosphere to unite with other elements and thus make it available for the use of green plants. This union of free (gaseous) nitrogen with some other element or elements to form a compound is called nitrogen fixation. The principal processes by which nitrogen fixation takes place in nature are (1) electrical discharges in the atmosphere, (2) activity of bacteria living free in the soil, and (3) activity of bacteria living symbiotically in the roots of certain plants. The quantity of fixed nitrogen which is added to the soil by the first of these processes is negligible.

There are two distinct groups of nitrogen-fixing bacteria: (1) non-symbiotic forms, and (2) symbiotic forms. The non-symbiotic nitrogen-fixing bacteria live free in the soil and have the power of combining the nitrogen of the air in the soil with other elements and thus building up the complex organic nitrogen compounds of their own cells. These complex compounds are later broken down by soil bacteria with the formation of nitrates. The best-known nitrogen-fixing bacteria living free in the soil are *Clostridium pasteurianum* and several species of *Azotobacter.*

The symbiotic forms live in the tissue of the roots of certain flowering plants, particularly members of the Leguminosae (bean family). The nitrogen-fixing bacterium which is commonly found in the roots of various beans, peas, lupines, clovers, and other leguminous plants is *Pseudomonas radicicola.* There are, however, several different strains of this microorganism, certain of which thrive only when associated with one or a few species of leguminous

plants. These bacteria generally gain entrance to the roots when the latter are young through a root hair and by their presence cause the formation of swellings or tubercles upon the root (Fig. 179). The cells of these tubercles are largely filled with bacteria. The atmos-

FIG. 179. Base of a plant of scarlet runner bean (*Phascolus multiflorus*) showing root tubercules which contain symbiotic nitrogen-fixing bacteria.

pheric nitrogen is probably fixed by these organisms into organic nitrogen compounds. The plant bearing the tubercles is able to absorb and utilize this organic nitrogen or some simpler nitrogen compound arising from its partial decomposition. Leguminous plants growing in nitrogen-poor soil from which the proper strain of *Pseudomonas radicicola* is lacking may be much stunted, but in the same soil in the presence of such bacteria they will thrive. Even after the removal of such a crop grown in association with the symbiotic nitro-

gen-fixing bacteria, the soil contains much more fixed nitrogen than before the infected legume crop was grown in it. The relation between *Pseudomonas radicicola* and the leguminous plant is certainly to be considered as one of symbiosis (living together of two kinds of organisms with mutual benefit). The bacteria secure food from the protoplasm of the leguminous plants in whose roots they live, and the legume secures nitrogenous compounds from the bacteria.

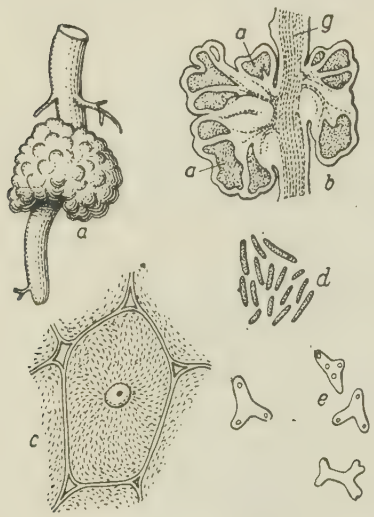


FIG. 180. Root tubercles from a lupine plant (*Lupinus*). *a*, exterior view 5 times natural size. *b*, longitudinal section showing at *a* the tissue filled with bacteria. *c*, a cell from *a* filled with nitrogen-fixing bacteria but still containing the nucleus of the root cell (magnified 200 times). *d*, nitrogen-fixing bacteria from a root tubercle. *e*, bacterioids (modified forms of bacteria in old tubercles). *d* and *e*, enlarged 1000 times. (After Fischer.)

Nitrification. — Considerable ammonia is liberated in the soil as a result of the decay there of proteins from dead organisms, both plant and animal, or their organic products. If this remained in the form of ammonia gas it might diffuse into the atmosphere and thus be lost to the soil in which it was produced. Actually most of it is combined in the soil with other substances to form salts, such, for instance, as ammonium carbonate, $(NH_4)_2CO_3$. Ammonium nitrogen is generally changed by bacteria in the soil into the nitrate nitrogen of such compounds as potassium nitrate and calcium nitrate, (KNO_3 or $Ca(NO_3)_2$). This change is known as nitrification and is a process of great importance since nitrates are apparently a much better source of nitrogen for crop plants than are ammonium compounds. The transformation is known to take place in two stages: (1) the conversion of ammonium nitrogen into the nitrogen of nitrites, such as potassium nitrite, KNO_2, and calcium nitrite, $Ca(NO_2)_2$; and (2) the conversion of nitrites into nitrates. The two stages are carried on by different bacteria. Several species of the genus *Nitrosomonas* are

known to be able to bring about the first step, and the second may be accomplished by bacteria belonging to the genus *Nitrobacter*. These two kinds of organisms always occur together and are common in soils and river water. As rapidly as nitrite is formed by *Nitrosomonas* it is converted into nitrate by *Nitrobacter*, so that

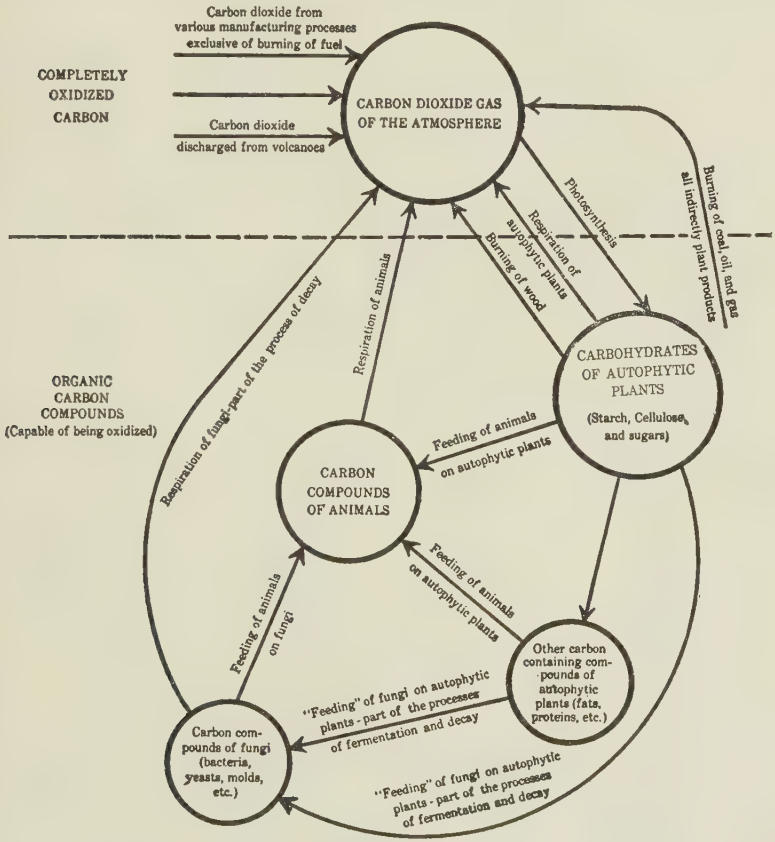

Carbon dioxide from various manufacturing processes exclusive of burning of fuel
COMPLETELY OXIDIZED CARBON
Carbon dioxide discharged from volcanoes
CARBON DIOXIDE GAS OF THE ATMOSPHERE
Photosynthesis
Respiration of autophytic plants
Burning of wood
Burning of coal, oil, and gas all indirectly plant products
CARBOHYDRATES OF AUTOPHYTIC PLANTS (Starch, Cellulose, and sugars)
Respiration of animals
Respiration of fungi-part of the process of decay
ORGANIC CARBON COMPOUNDS (Capable of being oxidized)
Feeding of animals on autophytic plants
CARBON COMPOUNDS OF ANIMALS
Feeding of animals on autophytic plants
Feeding of animals on fungi
Other carbon containing compounds of autophytic plants (fats, proteins, etc.)
"Feeding" of fungi on autophytic plants - part of the processes of fermentation and decay
Carbon compounds of fungi (bacteria, yeasts, molds, etc.)
"Feeding" of fungi on autophytic plants - part of the processes of fermentation and decay

FIG. 181. Carbon cycle diagram, showing the principal sources of the carbon dioxide of the atmosphere and the principal changes which it may undergo in organisms.

in some cases it is not possible to detect nitrites in soils in which nitrification is going on. The nitrite and nitrate bacteria belong to a very small physiological group of bacteria which can exist in the absence of any organic material in the medium in which they grow. They are able to manufacture their own organic food out of carbon dioxide, water, and other simple inorganic substances.

Thus they are very like green plants as far as their independence of other organisms is concerned. They can make their own food, however, in the absence of light and in this respect are in striking contrast with green plants. The reason for their difference is that

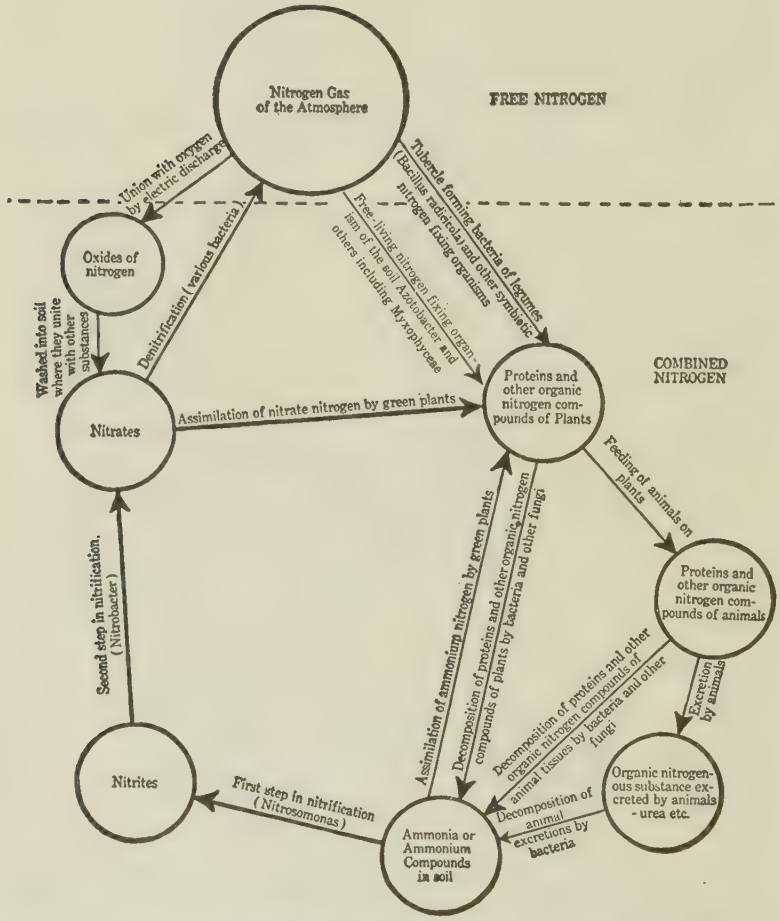

Nitrogen Gas of the Atmosphere
FREE NITROGEN
Union with oxygen by electric discharges
Tubercle forming bacteria of legumes (Bacillus radicicola) and other symbiotic nitrogen fixing organisms
Free-living nitrogen fixing organism of the soil Azotobacter and others including Myxophyceae
Oxides of nitrogen
Washed into soil where they unite with other substances
Denitrification (various bacteria)
Nitrates
Assimilation of nitrate nitrogen by green plants
Proteins and other organic nitrogen compounds of Plants
COMBINED NITROGEN
Feeding of animals on plants
Proteins and other organic nitrogen compounds of animals
Assimilation of ammonium nitrogen by green plants
Decomposition of proteins and other organic nitrogen compounds of plants by bacteria and other fungi
Decomposition of proteins and other organic nitrogen compounds of animal tissues by bacteria and other fungi
Excretion by animals
Second step in nitrification. (Nitrobacter)
Nitrites
First step in nitrification (Nitrosomonas)
Ammonia or Ammonium Compounds in soil
Decomposition of animal excretions by bacteria
Organic nitrogenous substance excreted by animals - urea etc.

FIG. 182. Nitrogen cycle diagram, showing the principal changes in form which nitrogen may undergo in organisms.

the nitrifying bacteria secure the energy for making their carbohydrates and other foods from the chemical energy liberated by the oxidation of ammonium nitrogen to nitrite nitrogen and of nitrite nitrogen to nitrate nitrogen. This process of food manufacture by

the use of energy secured from a chemical change is called **chemosynthesis** as contrasted with photosynthesis.

Denitrification.—There have been found in soil and in manures, as well as in the air and in natural bodies of water, bacteria which, instead of increasing the quantity of nitrate nitrogen, carry on the reverse process and convert nitrates into nitrites or gaseous oxides of nitrogen, or even into free nitrogen. If this process of denitrification results in the formation of free nitrogen, the nitrogen passes into the air and is lost from the soil.

The Carbon Cycle and the Nitrogen Cycle.—As we have learned in earlier chapters, autophytic plants build up the simple inorganic substances, water, carbon dioxide, and salts containing calcium, potassium, magnesium, iron, sulphur, nitrogen, and phosphorus into relatively complex organic substances which constitute the food not only of these green plants but also of all animals and heterophytic plants. These organic substances are broken down again in the destructive process, respiration, which goes on in all living organisms. In the dead bodies of plants and animals and in the excretions of animals there are large quantities of carbon, nitrogen, and the other essential elements (in the form of organic compounds) which are not available for the use of green plants. Various bacteria and other fungi can "unlock" the organic compounds of dead plants and animals, and of the excretions of animals, and convert the essential elements into forms in which they can be used again as raw material for food manufacture by autophytic plants. Thus it is that these elements pass repeatedly through a cycle in which they are first converted from simple to complex compounds and then returned to the simple form by respiration or by fermentation by bacteria and other fungi. If we could trace the history of any nitrogen or carbon atom, for instance, we might find that it had been part of hundreds of different organisms in succession; that it had literally "transmigrated" from an oak, to a bacterium, to a wheat plant, to a man, to a worm, and thus through innumerable changes throughout the ages since life first appeared upon the earth. The principal changes which carbon and nitrogen may undergo in one such cycle are graphically shown in the accompanying diagrams (Figs. 181 and 182).

MYXOMYCETES, OR SLIME FUNGI

Characteristics of the Myxomycetes.—In the Myxomycetes, a most remarkable group of plants, there seems to be a combination of animal and plant characteristics, and on this account these organisms have excited the interest of both botanists and zoologists. During the vegetative part of their existence these plants consist of multinucleate masses of naked protoplasm, termed **plasmodia** (singular **plasmodium**); they are capable of **amoeboid** move-

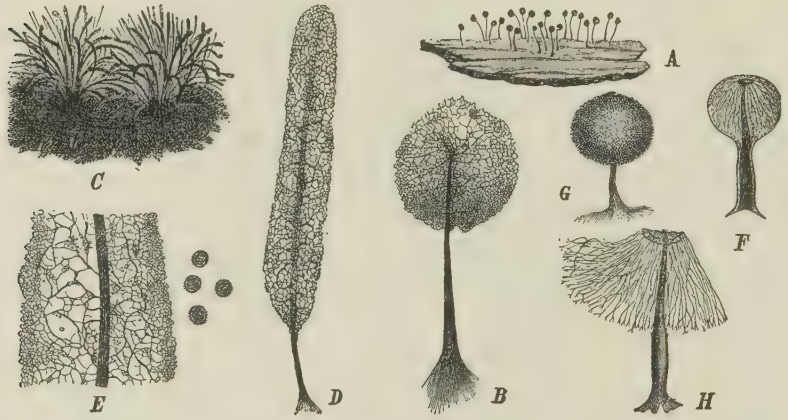


FIG. 183. Myxomycetes. *A-B. Comatricha nigra*; *A*, group of sporangia, natural size; *B*, a single sporangium enlarged showing the stalk and the net-like capillitium. *C-E, Stemonitis fusca*; *C*, sporangia, natural size; *D*, a single sporangium enlarged showing the stalk and capillitium; *E*, portion of capillitium and spores. *F-H, Enerthema papillatum*; *F*, unripe sporangium; *G*, mature sporangium; *H*, *capillitium*. (*C, D,* after Harshberger. *A, F, G, H,* after Rostafinski; *B, E,* after de Bary; all from Harshberger's *Mycology and Plant Pathology*.)

ment (movement by flowing) of arm-like portions of the protoplasm, known as **pseudopodia**, and they can flow around and engulf solid food particles. These characteristics—absence of cell walls, locomotion by streaming of protoplasm, and ability to take solid food particles into the protoplasm—are generally considered to be animal characteristics. In their reproduction, however, the Myxomycetes are more like certain plants (some kinds of fungi) than they are like any animals, and their spores have cellulose walls, another plant characteristic. With the exception of two or three parasitic genera, such as *Plasmodiophora* which causes the disease known as "club root" of cabbage and other crucifers, they are all

saprophytes, securing their food from the decaying leaves and twigs and rotting wood of moist habitats, mostly the forests. Because of their delicate structure and occasionally brilliant coloring, many of the Myxomycetes are of remarkable beauty.

PHYCOMYCETES (ALGA-LIKE FUNGI)

To this group of fungi belong the water molds, the mold which causes the well-known "white rust of mustards," common bread

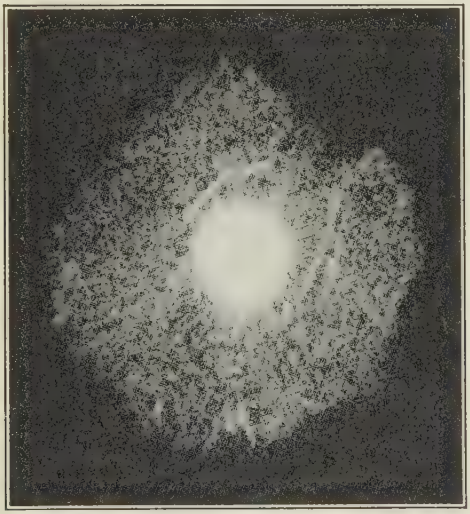


FIG. 184. Growth of *Saprolegnia* on a bit of dead organic matter.

mold, and the downy mildews. This class of fungi is called the Phycomycetes (literally, alga-like fungi) because of the close resemblance which they show to certain algae (1) in the structure of the filaments, **hyphae,** which make up the plant body, and (2) in their method of reproduction. The hyphae are like the filaments of some green algae (*Vaucheria,* e.g.), coenocytic tubes with no cross walls except where the reproductive organs are cut off; accordingly, the filaments are filled or lined with continuous multinucleate protoplasm. The absence of cross walls in the hyphae is characteristic, and by this vegetative feature alone they can usually be distinguished from the sac-fungi (Ascomycetes), and the

basidium fungi (Basidiomycetes), both of which groups have septate hyphae (with cross walls separating uninucleate or multinucleate cells). The group includes both parasitic and saprophytic species.

There are two sub-classes of Phycomycetes, the Oomycetes, and the Zygomycetes. Most of the Oomycetes are aquatic, or at least at some portion of their life are dependent upon water for spore distribution, because of the development of motile asexual spores (zoospores), whereas the Zygomycetes are principally aerial and produce non-motile spores. The Oomycetes are heterogamous, producing unlike gametes which unite to form an oospore. The Zygomycetes are isogamous, the gametes being similar and uniting to form a zygospore.

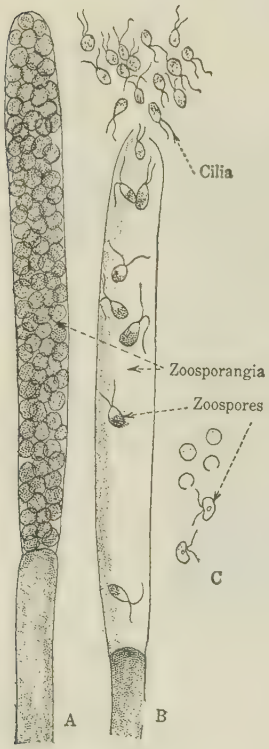


FIG. 185.

Saprolegnia (Water Mold.)—Most of the species of *Saprolegnia* (which belongs to the Oomycetes) are saprophytic on the bodies of dead insects and crustaceans or on other decaying organic matter. A few species are parasitic and attack living fish or fish eggs, sometimes being very destructive when they infest the eggs and young fish in hatcheries.

The hyphae penetrate the substratum (material upon which the mold grows) and absorb organic substances which they use as food and which make possible the growth of the organism. As in certain algae, some of the hyphae which protrude into the surrounding medium become swollen at the tip, and cross walls are formed, separating the swollen portions from the rest of the hypha. This terminal structure becomes a **sporangium**, its contents dividing up into a large number of zoospores, each having a single nucleus and two cilia borne at one end. A peculiarity of *Saprolegnia* is that each one of these zoospores, instead of germinating to form new hyphae, comes to rest and forms a wall, the protoplast then escaping and forming again a single biciliate zoospore, which in

turn gives rise to new filaments. The significance of the two different zoospore stages is not clear.

The sexual reproduction is heterogamous and similar to that of the green alga, *Vaucheria*. Each oogonium (female gametangium) is a spherical structure, the contents of which form one or

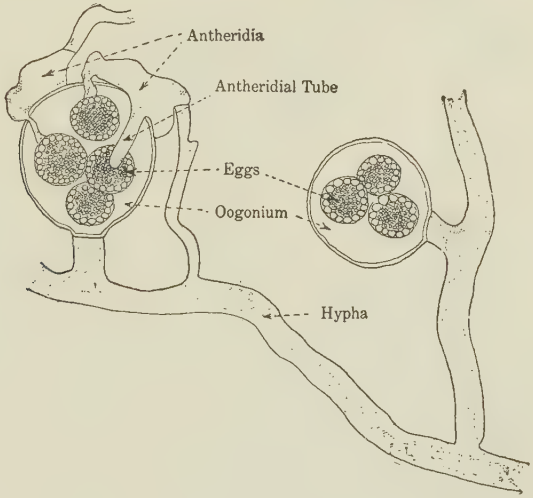


FIG. 186. Sexual reproduction in *Saprolegnia*. (Redrawn from Sinnott in *Botany*, McGraw-Hill Book Co., Inc.)

more eggs (female gametes). The antheridia (male gametangia) arise on branches near the oogonia. They are tubular in form and curve so that they come in contact with the oogonia. A slender tube (fertilization tube) is then sent out from the antheridium and penetrates the wall of the oogonium. A separate antheridium and fertilization tube are necessary for the fertilization of each egg. The contents of the antheridium consist of a non-motile male gamete. This is discharged into the oogonium and fertilization results, after which the eggs form thick-walled oospores which, upon germination, form new hyphae directly.

Albugo candida.—This is a parasite attacking members of the mustard family (Cruciferae), and causing a disease known as "white rust." The principal symptoms of the disease are distortions and enlargements of the flower clusters and fruits, and the development of porcelain-white blotches or blisters on the leaves

and stems. The **mycelium** (collective name for the vegetative hyphae of a fungus) occupies the intercellular spaces within the tissues of the host, and sends out small, slender lateral projections called **haustoria,** which penetrate the cell walls, enter the cells,

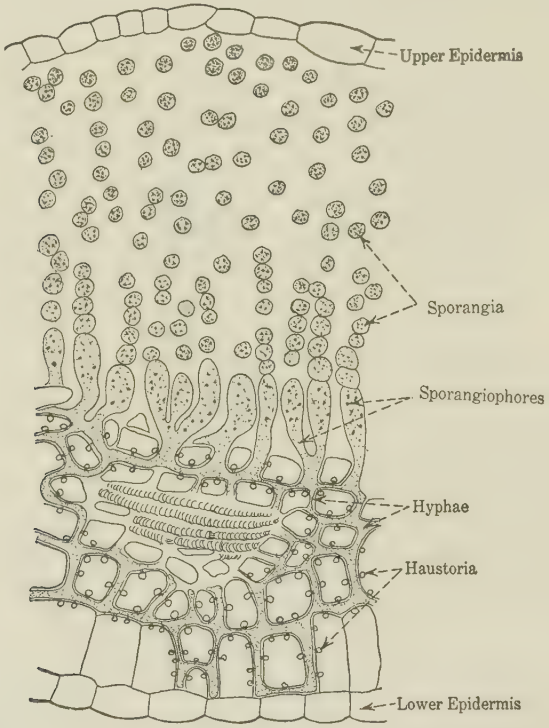


FIG. 187. Cross section of leaf of shepherd's purse (*Capsella*) parasitized by "white rust" of crucifers (*Albugo candida*) and showing the hyphae with their knob-like haustoria, the erect sporangiophores, and multinucleate sporangia. Note that by growth of the sporangiophores and sporangia the epidermis is being torn from the underlying mesophyll. (Redrawn from Chamberlain.)

become swollen at the tips, and act as absorbing organs. Chains of asexual, multinucleate bodies, known as **sporangia,** are produced under the epidermis of the host, by constrictions of erect hyphal branches, known as **sporangiophores.** Each of these non-motile, multinucleate sporangia breaks up into many motile zoospores which in time escape, and then germinate to form a new mycelium.

Heterogamous sexual reproduction also occurs. Large spherical oogonia are produced, each of which forms a single female gamete.

From neighboring hyphae are produced elongated antheridia, each with a fertilization tube. The tube penetrates the oogonial wall, and through this tube passes a single male nucleus which unites with the egg nucleus. The oospore is a resting body; on germination it develops zoospores or produces a mycelium directly.

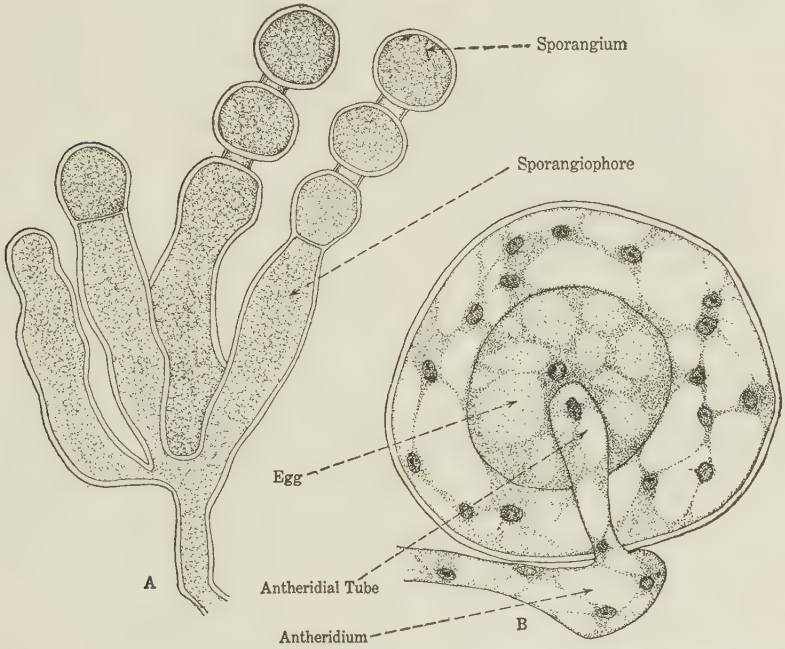


FIG. 188. "White rust of crucifers" (*Albugo candida*). *A*, showing development of sporangia. *B*, fertilization.

"Downy Mildews."—These parasitic fungi, belonging to the Oomycetes, cause serious diseases, such as the "late blight" of potatoes and the downy mildew of grapes and of other plants. It is of interest to note that the serious famine of Ireland in 1845 was largely due to the failure of the potato crop resulting from the attacks of the "late blight." The fungus spreads very rapidly by means of sporangia, which are borne singly at the tips of branched sporangiophores. These sporangia may germinate directly into new hyphae, or they may form zoospores when they germinate.

Rhizopus nigricans (Common bread mold).—This is the best-known representative of the Zygomycetes. It is very commonly

found growing on stale bread when it is kept moist, decaying fruit and vegetables, and other organic materials left exposed to the air in moist places. *Rhizopus* spores are almost always present in the atmosphere except just after a heavy rain or snow storm when the air is almost free of bacteria and fungus spores.

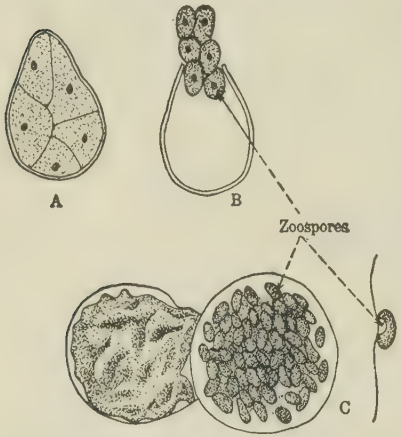


FIG. 189. "White rust" of crucifers (*Albugo candida*). *A*, sporangium, the protoplasmic contents of which have divided preparatory to zoospore formation. *B*, zoospores, with cilia not yet extended, escaping from sporangium. *C*, germinating zygote discharging the numerous zoospores which for a time are surrounded by a membrane. (*C*, redrawn from de Bary.)

The mycelium consists of profusely branching coenocytic hyphae, which grow upon and within the substratum which supplies the necessary foods. Certain hyphae, called **stolons**, of larger diameter than those which are formed within the substratum, grow just above its surface for a short distance, coming into contact with the substratum here and there along their length. At the points of contact there are produced clusters of hyphal branches which

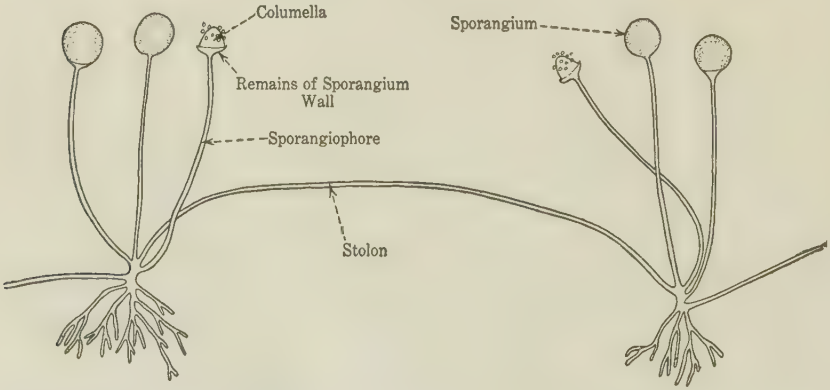


FIG. 190. Bread mold (*Rhizopus nigricans*), showing groups of sporangiophores, rhizoid-like branches, and stolons.

penetrate the material upon which the fungus is growing and con-

stitute holdfasts which somewhat suggest in their appearance the roots of higher plants. Later there arise at these points groups of erect branches, sporangiophores, upon which the sporangia are produced. The spores are non-motile, multinucleate, and surrounded

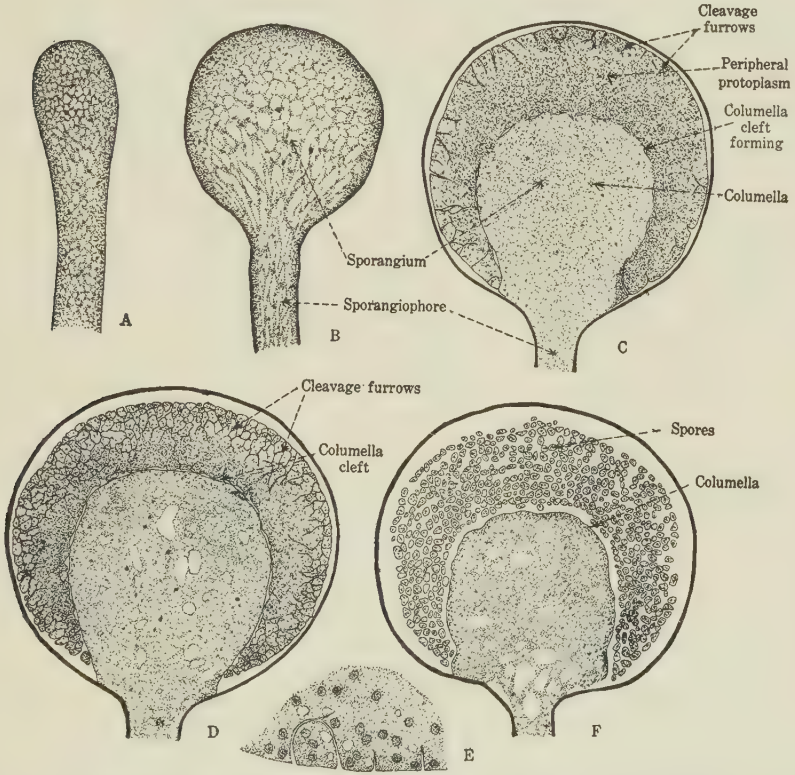


FIG. 191. Stages in the development of the sporangia and in the formation of the spores of *Rhizopus nigricans* (black bread mold) as seen in longitudinal sections. *A* and *B* show the enlargement of the free end of a sporangiophore to form the sporangium. *C, D,* and *F* show the formation of the columella, and of the spores by furrowing of the cytoplasm between the columella and the sporangium wall. *E* shows in greater detail a small portion of the protoplasm of the sporangium represented in *C*. (Redrawn from D. B. Swingle's paper, Bureau of Plant Industry, Bulletin 37.)

by a thick, black, cellulose wall. The method of their formation and release from the sporangia is shown by Figs. 190 and 191.

In sexual reproduction, pairs of club-shaped hyphal branches are formed which come into contact at their tips (Fig. 192). The mass of dense protoplasm in the tip of each of these branches is cut

off by a cross wall. The enclosed compartments thus formed are the gametangia (gamete-bearing organs), and the mass of multinucleate protoplasm enclosed in each is a **coenogamete.** After dissolution of the walls of the gametangia at the point of contact, the two adjoining coenogametes unite, the nuclei from the two coenogametes fusing in pairs. Inasmuch as the two fusing masses are alike in structure, the fusion is spoken of as conjugation although it differs from ordinary conjugation where two similar, uninucleate gametes fuse. The zygospore thus formed develops a thick, black

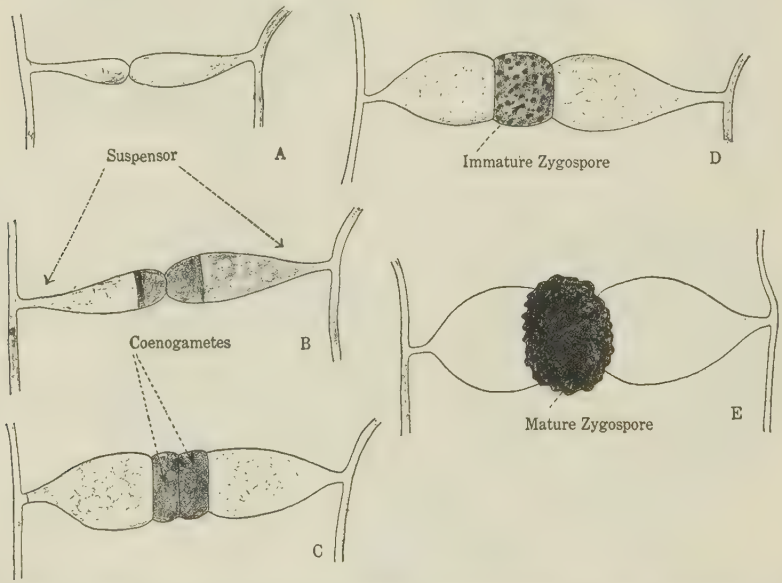


FIG. 192. Bread mold (*Rhizopus nigricans*), showing stages in the formation of the zygospore.

wall about itself. After a resting period the zygospore may, under favorable external conditions, germinate and send out a single sporangiophore, at the tip of which a sporangium containing asexual spores is formed. In *Rhizopus nigricans,* conjugation does not take place between any two hyphae which happen to be adjoining. There are two strains or races of *Rhizopus nigricans,* designated as the "minus strain" and the "plus strain." Both strains must be present and the conjugating hyphae must be one of one strain and one of the other, otherwise conjugation will not take place. Thus,

there seems to be some physiological sexual differentiation although the gametes appear alike except for a slight difference in size. Sexual reproduction is not essential to the persistence of *Rhizopus,* for the plant may propagate itself indefinitely by means of the asexual spores. There are many localities in which only one of the two strains of *Rhizopus* occur, and, although the mold may thrive in such regions, zygospores are never formed.

Phycomycetes—A Summary.—The group includes both parasitic and saprophytic forms. The hyphae are characteristically coenocytic and non-septate. Asexual reproduction is by spores, which may be non-motile or motile (zoospores). In sexual reproduction the gametes may be similar and unite to form a zygospore, or unlike and unite to form an oospore. Some Phycomycetes (water molds) are dependent, at least during some portion of their life, upon water for spore distribution, whereas other Phycomycetes (*Rhizopus*) are principally aerial and produce non-motile spores.

Fig. 193. Sporangiophore and sporangium of *Rhizopus* developed from zygote; note wall of zygote.

ASCOMYCETES (SAC FUNGI)

The Ascomycetes form the largest group of fungi and include a great variety of forms, many of which are of importance because they cause diseases of economic plants. In addition to many important parasitic Ascomycetes causing plant diseases, the group includes also such non-parasitic forms of economic significance as the blue and green molds (so common on preserves and decaying fruit), the yeasts, and the truffles. Several species of a blue mold belonging to the genus *Penicillium* are of use in the manufacture of certain kinds of cheese. For example, *Penicillium roqueforti* is the active agent in the ripening of Roquefort, Gorgonzola, and Stilton cheeses, and *Penicillium camemberti* in ripening Camembert cheese. The great economic importance

of yeast in bread making, in brewing, and in other processes in which sugar fermentation is essential is well known. Truffles produce underground, tuber-like fruiting bodies, usually associated with the roots of oak trees. They are highly prized as a food delicacy, and in certain parts of Europe dogs and swine are trained to locate truffles in the forest.

The one outstanding characteristic of the group, and the one that suggested the name Ascomycetes, is the formation, somewhere

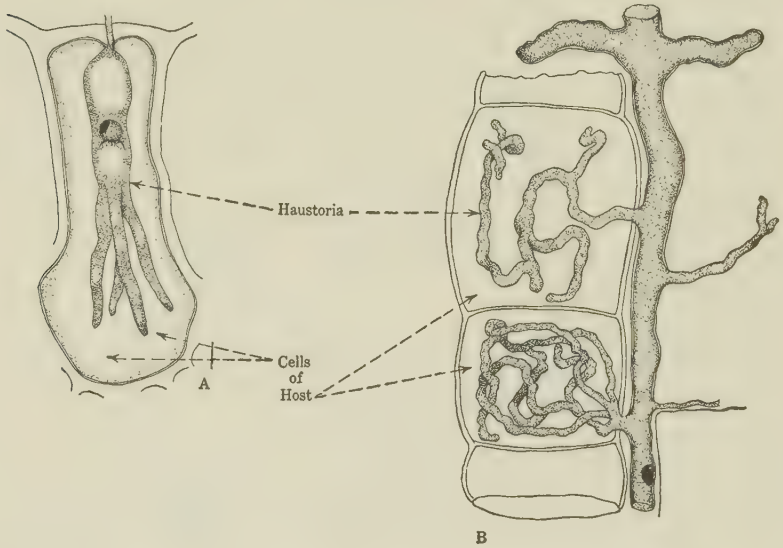


FIG. 194. Haustoria of (*A*) a powdery mildew fungus (*Erysiphe graminis*) and (*B*) a downy mildew fungus (*Peronospora*). (*A* redrawn from C. C. Curtis, *B* from Smith.)

in the life history, of sac-like hyphae called **asci** (singular **ascus**) within each of which are produced a number of spores (generally eight) called **ascospores.** The hyphae of the Ascomycetes differ from the coenocytic hyphae of the Phycomycetes in being septate, that is, divided by transverse walls into cells, each of which may contain one or more nuclei. In most Ascomycetes the asci are produced in special, often large and fleshy, fruiting bodies called **ascocarps.** In *Peziza* and *Sclerotinia* the asci are borne in a cup-shaped or saucer-shaped ascocarp which is called an **apothecium.** In the powdery mildews the asci are formed within a more or less

spherical ascocarp called a perithecium, which is entirely closed. Thus ascocarps are either apothecia or perithecia.

Representatives of the Ascomycetes.—*Cup Fungi.*—One of the commonest types of saprophytic Ascomycetes is *Peziza,* which generally grows in soil very rich in organic matter, or on decaying wood. There arises from the mycelium a conspicuous apothecium (open ascocarp) which is in the form of a cup and in some cases

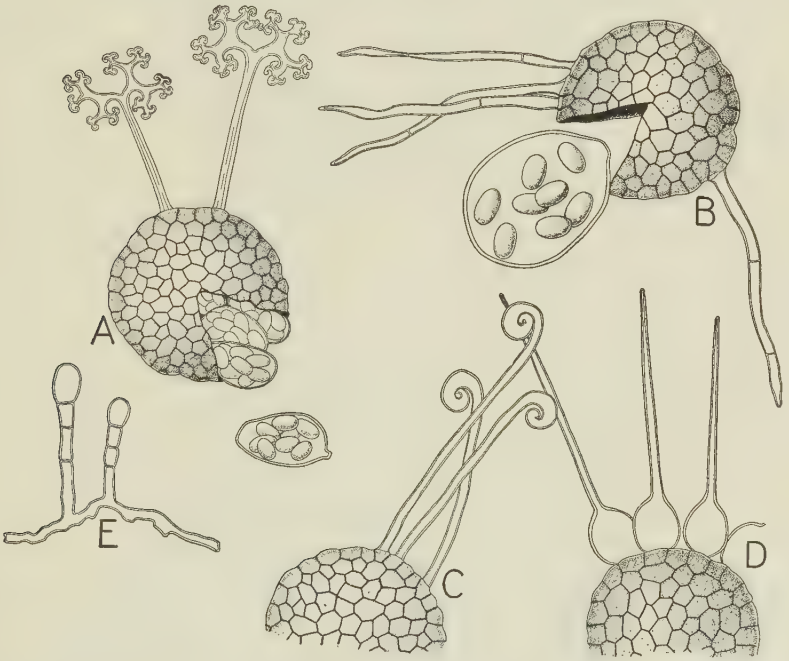


FIG. 195. Fruiting stages of various genera of powdery mildew fungi. *A*, perithecium of *Microsphaera* from lilac leaf; *B*, perithecium of *Sphaerotheca* from gooseberry; *C*, perithecium of *Uncinula* from willow; *D*, perithecium of *Phyllactinia* from dogwood; *E*, conidial stage of a powdery mildew fungus growing on red clover. (After Owens, from *Principles of Plant Pathology.*)

is brightly colored within. In one species, *Peziza aurantia,* the inner surface of the cup is bright orange in color. A section through the hymenium (tissue lining the interior of the cup) shows numerous cylindrical asci, each containing eight ascospores, and intermixed with the asci numerous sterile branches or hyphae known as paraphyses. The asci and paraphyses are perpendicular to the surface of the hymenium and parallel to each other.

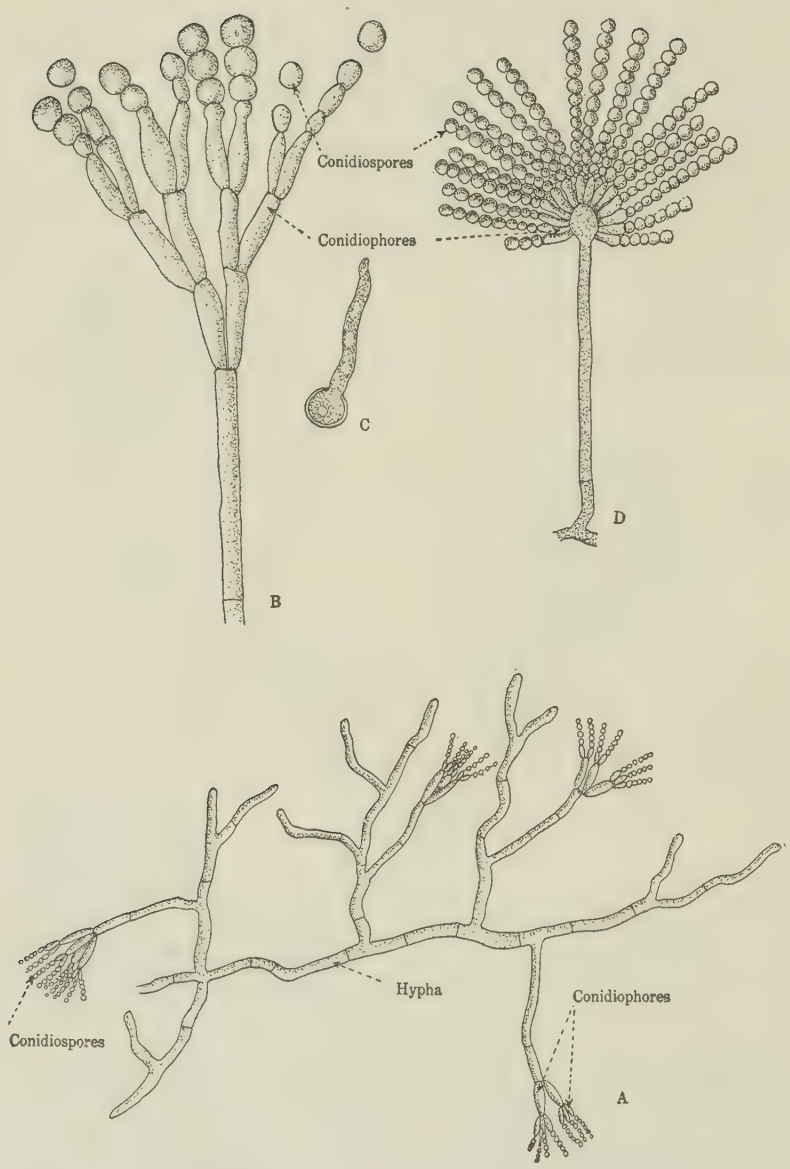


FIG. 196. Blue and green molds. *A* and *B*, common blue mold (*Penicillium*). *C*, germinating conidiospore. *D*, green mold (*Aspergillus*).

No sexual reproduction has been found in *Peziza*, but it is known to occur in related forms. The union of a male and a female coenogamete results in a zygote which sends out a number of hyphae, at the tips of which the asci are developed. The paraphyses which are intermingled with the asci arise from beneath the oogonium. Other sterile hyphae form the cup-shaped ascocarp.

Powdery Mildews.—The **"powdery mildews"** constitute a large family of ascomycetes, all of which are strictly parasitic. Many crop plants are afflicted with some one of these mildews. They

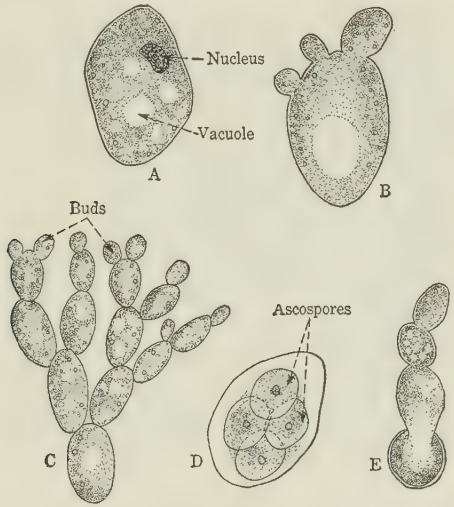


FIG. 197. Yeast (*Saccharomyces cerevisiae*). *A*, single cell highly magnified. *B*, cell in process of budding. *C*, chain of cells formed as result of rapid budding and growth. *D*, formation of ascospores. *E*, germination of ascospore and the development of new plants by budding. (Redrawn from Curtis.)

produce their mycelium on the surface of the host. The hyphae bear **haustoria**, which penetrate the host cells. Asci are developed in perithecia (closed ascocarps), and the conidiospores which are produced in chains on the surface of the host are often present in such immense numbers as to give a mealy or powdery appearance to the diseased structures.

Blue and Green Molds.—The **blue and green molds** are well-known saprophytic ascomycetes found on a great variety of substances. *Aspergillus* and *Penicillium* are the two most common genera. *Aspergillus* species occur on decaying vegetables of all sorts,

on moldy cereals, on jellies, old leather, etc. The mycelium produced is prolific, and spores arise in enormous numbers. Spores are developed on conidiophores, and arise by abstriction of terminal branches. The characteristic color of the mold appears when the conidiospores develop; in the different species they are various shades of green, brown, yellow, and red. The conidiospores, which are carried by air currents, and which when in abundance impart a characteristic moldy odor to the atmosphere, are capable of immediate germination if they fall upon the proper substratum.

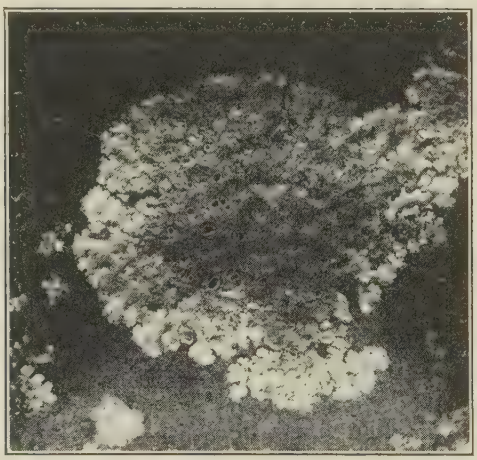


FIG. 198. A foliose lichen showing the cup-shaped apothecia.

Penicillium is the common blue mold on bread, cheese, lemons, etc. The conidiophores are branched, each branch bearing a chain of conidiospores. Sexual reproduction has been observed in several species of both *Aspergillus* and *Penicillium*.

Yeasts.—The yeasts are usually included with the Ascomycetes because of their production, under certain conditions, of structures which sometimes resemble asci.

The beer, alcohol, and wine yeasts are included in the genus *Saccharomyces*, which has a number of species. *Saccharomyces cerevisiae* is by far the most important species, being the one employed in beer brewing and bread making.

Yeast cells may remain attached in short chains but they do not produce a true mycelium. The cells are usually egg-shaped

or spherical, and each cell is surrounded by a well-defined wall. Within the yeast cell are the nucleus (not visible without staining the cells), oil globules, and vacuoles.

One of the chief characteristics of the yeasts is their method of vegetative reproduction by "budding." In this process a portion of the protoplasm of a cell surrounded by a cell wall forms a lateral outgrowth (bud), which finally may separate from the parent cell, and thus a new individual is produced.

Ascospores are produced only when there is an abundance of oxygen. In the production of ascospores the cell nucleus divides into several daughter nuclei, each one of which becomes the center of a spore lying within the original cell. The number of spores developed in a single yeast cell varies, but it is usually four. On disintegration of the wall of the original cell, the spores are liberated, and under proper conditions produce new colonies of yeast plants.

The most important characteristic of the yeasts is their power of causing alcoholic fermentation. The yeast cells absorb certain sugars, and within the protoplast the sugar is decomposed with the formation of carbon dioxide and ethyl alcohol. This change is due to the presence in the yeast cells of the enzyme zymase, which is a product of the protoplasm.

The great economic importance of yeast is realized when we understand that, because of its power of producing a sugar-fermenting enzyme, it is indispensable in the making of bread, in the manufacture of commercial ethyl alcohol, and in the production of alcohol in fermented liquids used as beverages.

In bread making, yeast plants are mixed with flour and water. The flour contains some sugar in addition to the starch. At a suitable temperature, the yeast cells multiply rapidly. Zymase is formed, which aids in the breaking down of the sugar into alcohol and carbon dioxide. The bubbles of carbon dioxide gas are prevented from escaping by the dough, which, however, is caused to rise by the expansion of the bubbles. At baking temperatures there is further expansion of the gas bubbles, and also a driving off of alcohol and water.

Lichens.—The lichens constitute one of the most extraordinary groups of plants to be found in the plant kingdom. Lichens are world wide in distribution. They are found in a great variety of situations, and are of many different forms and colors. Crustaceous

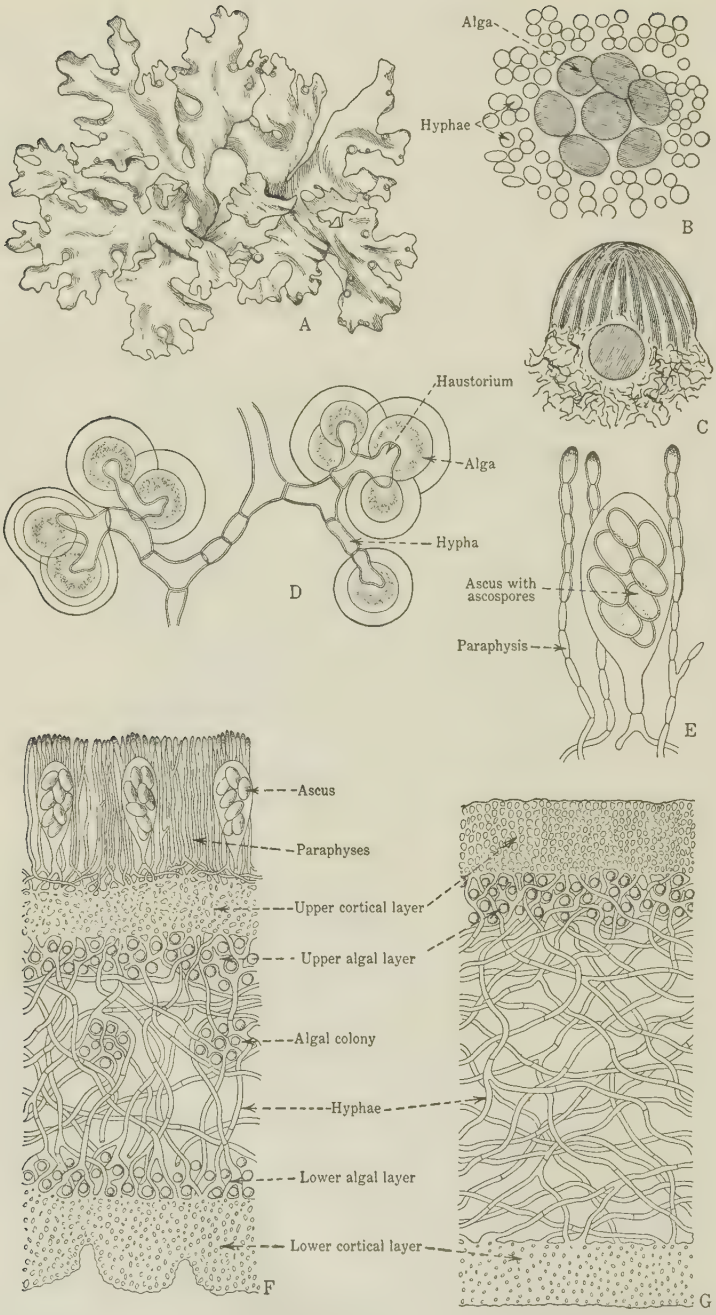


FIG. 199. A lichen. *A*, plant slightly reduced. *B* and *C*, soredia in different stages of development. *D*, algal cells surrounded by fungal cells with haustoria. *E*, three paraphyses and a single ascus. *F*, section of apothecium. *G*, section of vegetative portion of thallus. (*B* and *C*, after Schwendener; *E*, *F*, and *G*, after Schneider; *D*, after Bornet.)

and leaf-like forms occur on the surface of rocks, on the bark of trees, and on the soil. Some lichens, such as the so-called reindeer moss (*Cladonia*) of arctic tundras, grow to a length of several inches. In many habitats, lichens are exposed to the greatest extremes of temperature and humidity. In fact they are able to live in habitats—exposed rocks and tree bark, for example—where few other plants can maintain themselves. They will undergo extreme desiccation for a long period, and revive when favorable conditions recur.

The remarkable thing about the lichens is that the plant body is always made up of two different species growing together, one an alga, generally a green alga but sometimes a blue-green alga, and the other a fungus, generally an ascomycete. Neither the fungus nor the alga if grown alone shows any resemblance to a lichen, but when the algal species and the fungus species exist together in a relationship of symbiosis a characteristically formed and colored "compound organism" results which may be very successful in the struggle for existence even under conditions highly unfavorable to most plants.

Food is manufactured by the algal component of the lichen for its own use and for that of the fungus component as well. The fungus, on the other hand, probably serves the alga principally by absorbing and holding moisture. In addition to vegetative multiplication of the lichen, the fungus can reproduce itself separately by the formation of ascospores.

Ascomycetes—A Summary.—The group includes both parasitic and saprophytic forms. Many important diseases of cultivated plants are caused by representatives of the group. The hyphae are septate, thus being distinguished from those of the Phycomycetes. The characteristic feature of the group is the formation, somewhere in the life history, of sac-like hyphae called asci, within each of which are produced a number of spores, called ascospores. The asci are generally produced in fruiting bodies, known as ascocarps, which may be open (apothecia) or closed (perithecia).

BASIDIOMYCETES (BASIDIUM-FORMING FUNGI)

This large group of fungi includes such well-known representatives as the smuts, the rusts, and certain fleshy and woody fungi, many of which commonly go under the names of "mushrooms" and

"toadstools." The group includes both parasitic and saprophytic species. The class name is descriptive of the outstanding character of the group, which is the occurrence of a special type of conidiophore, called a basidium (plural basidia), in the life cycle of these

FIG. 200. 1, head of Little Club wheat affected with bunt or stinking smut (*Tilletia tritici*), and immediately to the right one kernel of wheat filled with chlamydospores of the parasite. 2, disease-free head of Little Club wheat, and to the left a normal wheat kernel. (From Mackie.)

plants. It is a club-shaped hypha which produces non-motile asexual spores, basidiospores, singly at the ends of several (usually four) slender, pointed protuberances called sterigmata (singular sterigma). In some genera the basidium is divided by cross walls into

a number of cells (generally four), but in other forms it is non-septate.

The hyphae which make up the mycelium are septate and branched. Gametangia have not been found, but simple nuclear fusions have been observed which probably correspond to fertilization.

The Smuts.—All the smuts are parasites. They occur on a wide range of hosts, the most common hosts being the Gramineae, which include the grasses and common cereals. The estimated

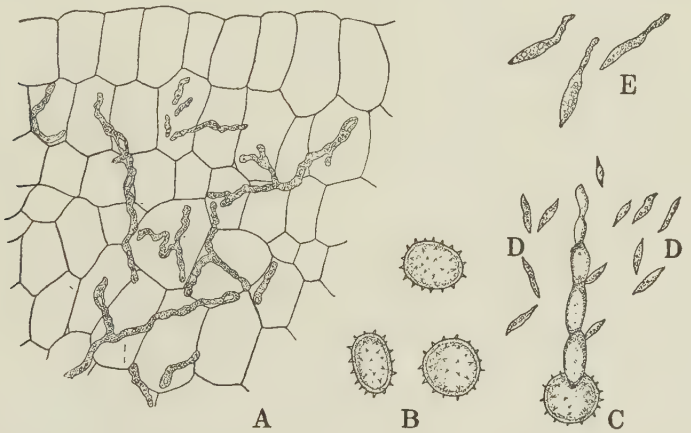


FIG. 201. Corn smut (*Ustilago zeae*). *A*, hyphae in the tissue of the host. *B*, mature chlamydospores. *C*, a germinating chlamydospore, showing the 4-celled basidium, two cells of which are producing sporidia (basidiospores). *D*, sporidia. *E*, budding sporidia. (Redrawn from Freeman and Stakman, in Minnesota Agricultural Experiment Station Bulletin.)

reduction of yield of cereals in the United States during 1921 due to smuts alone was 160,738,000 bushels.

The smut of corn, *Ustilago zeae*, may be selected as a type form. The mycelium of the fungus may be found in any part of the host, where it causes abnormalities and swellings, sometimes of considerable size. These "tumors" result from the abundant development of hyphae in the tissue of the host and from the resulting stimulation of the tissue of the affected organ to abnormally active growth. Later, practically all the internal tissue of the diseased part of the host is used up by the growth of the smut hyphae, so that the whole deformed structure, except the surface

layers, becomes a mass of fungal hyphae. These hyphae are then transformed into millions of black spores known as **chlamydospores.** Each of these spores is formed from a short segment of a hypha which becomes surrounded by a slightly thickened wall and then separates from the adjoining segments of the same hypha. Chlamydospores are capable of germination as soon as mature if conditions are favorable, or they may retain their vitality throughout the winter and germinate the next spring. Each germinating chlamydospore produces a short hypha, called a **promycelium** or **basidium,** which is divided by cross walls into three or four cells. Each of these cells bears a single basidiospore, which is generally spoken of as a **sporidium.** The sporidia are capable of saprophytic growth and multiplication by budding when appropriate organic matter is available. Such budding often goes on rapidly in barnyard manure. The sporidia are readily carried by the wind, and, if they fall upon any young tissue of a corn plant, they may send out short hyphae which may penetrate the epidermal cells and thus infect the plant.

In some species of smuts the chlamydospores adhere to the surface of the seeds and infection takes place in the seedlings which develop from the germinating seeds (bunt of wheat and oat smut). In other species, infection takes place through the ovary of the flowers so that the fungus hyphae are present in the embryos of the seeds when they ripen (loose smuts of wheat and barley). The proper treatment to reduce crop losses depends very largely upon what type of infection (seedling infection, flower infection, or general infection, as in corn) is characteristic of the particular smut species in question.

The Rusts.—The rusts are a group of fungi of great economic importance. They are parasites on a great variety of hosts, chiefly seed plants. Well-known diseases of economic plants which are caused by rusts are black stem rust of wheat, oats, barley, and rye, asparagus rust, apple rust, orange rust of raspberry and blackberry, and blister rust of pines. The grain losses due to the black stem rust of cereals are sometimes enormous. Many epidemics of this disease have occurred, those of 1904 and 1916 in this country having been particularly destructive. According to one of the principal American authorities on cereal rusts, "The most conservative estimate places the loss of wheat in the United States due to the

black stem rust in 1916 at 180,000,000 bushels, while the loss in Canada was estimated at about 100,000,000 bushels."

The rust fungi are striking examples of **obligate parasites**, that is, organisms which are unable to grow except on living tissue of some other organism. They are incapable of growing in culture media, even when the media are made from the host plant upon which they normally grow.

The mycelium is composed of septate hyphae which nearly always grow in the intercellular spaces of the host tissue and are branched and provided with haustoria. Spores are usually produced in patches, called **sori** (singular **sorus**), on the surface of the host. Five different types of spores may be formed in rust fungi, but not all are present in every species.

One of the best-known genera among the rusts is *Puccinia*. It has a number of economically very important species, chief of which is *Puccinia graminis,* the black stem rust of wheat, oats, barley, rye, and many grasses. The grain losses due to this parasite are sometimes enormous.

Most parasitic fungi require but a single host for their life cycle, but a few have two different host species and cannot complete their life cycle unless both are present. *Puccinia graminis* is one of the latter, requiring a grass such as wheat, as one host, and the barberry as the second or alternate host.

The first visible evidence of this rust on cereals is seen on stems and leaves as reddish-brown streaks or pustules, which make their appearance in the spring and summer. They are caused by groups (sori) of minute yellowish spores formed just beneath the epidermis of the host. These spores are known as **urediniospores** and the sori as **uredinia**. These spores give external evidence of the presence of a mycelium growing among the cells of the tissues of the host. The production of urediniospores is spoken of as the "red rust" stage of the disease. Each urediniospore is stalked, one-celled, and generally oval in form, and has a rather thick wall which bears numerous short, spiny projections. These spores are disseminated by the wind. They are capable of germination within four or five days after they are shed, if sufficient moisture is present. Infection takes place by the growth of the germ tube through a stoma into the host tissue. Within the host tissues this hypha branches and forms a new mycelial

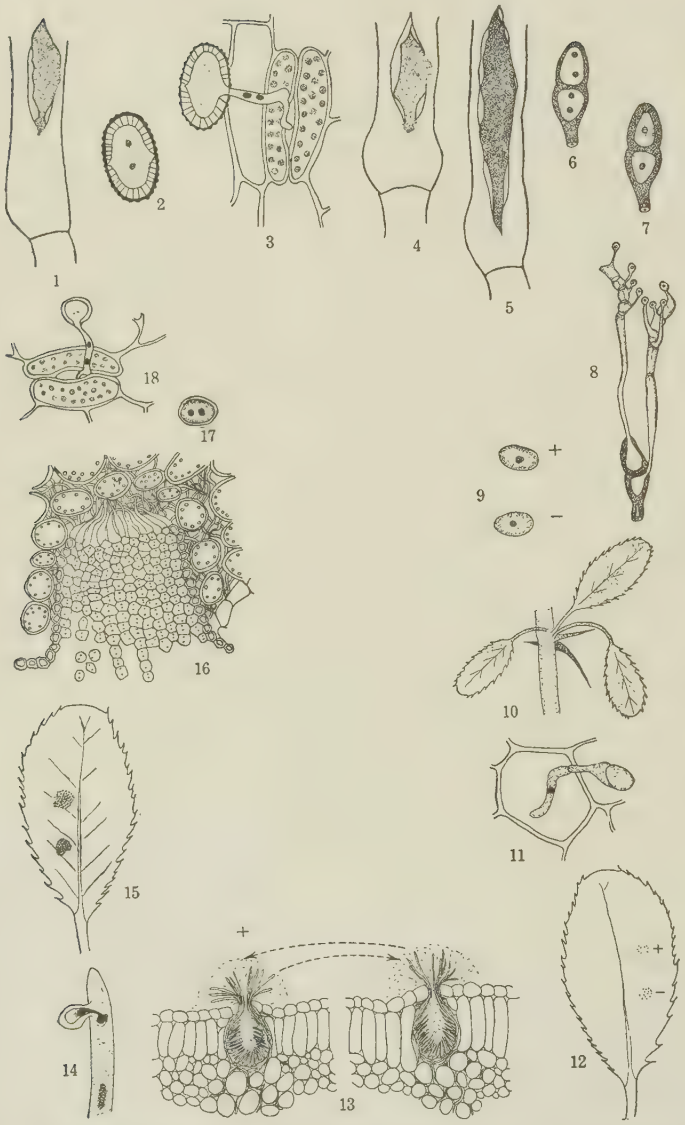


FIG. 202. Life cycle of black stem rust (*Puccinia graminis*)—an heteroecious rust. 1, Uredinia on wheat stem. The red urediniospores are produced early in the season. 2, A single urediniospore, a binucleate body. 3, Germinating urediniospore on the surface of the stem of the same or another wheat plant, its germ tube, with two nuclei, penetrating a stoma. As a result a mycelium, each cell of which is binucleate, is formed within the tissues of the host and soon another crop of urediniospores is borne in uredinia as shown in 4. Thus during a single season there may be successive crops of urediniospores, the disease thus spreading rapidly over a field. 5, A telium produced later on wheat stems. The teliospores which are liberated from the telia are 2-celled,

growth. Within a short time the mycelium absorbs sufficient food from the host to form a new crop of urediniospores. Thus it is possible to have a considerable number of successive crops of urediniospores in a single season, and from one or a few infected plants the disease may be spread over a large field.

Usually in the late summer or fall, when the grain begins to ripen, black pustules or sori appear on the same stems and leaves which produced the uredinia. These black sori consist of dark-colored spores known as *teliospores*. The sori are called *telia*. The teliospores are stalked, two-celled structures, which are spindle-shaped and have a thick wall. They are unable to germinate at once as do the urediniospores, but after wintering in the open on stubble or on the soil they germinate freely.

At germination one or both cells of the teliospores may send out a tube, which, as in the smuts, is called a promycelium or basidium. This is generally a four-celled structure, each cell of which forms a single colorless sporidium, **basidiospore**, on a short stalk or **sterigma**. The basidiospores are carried by the wind. They will not germinate and bring about infection unless they fall upon the leaves, twigs, or fruit of certain species of barberry, the most important of which is the common barberry (*Berberis vulgaris*). Here a germ tube is formed which penetrates the tissues of the plant, entering through a stoma.

Within seven to ten days after the barberry plants are infected by basidiospores there appear, submerged below the surface on the

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each cell being binucleate. They remain alive on the soil or straw during the winter. 6, A single immature teliospore, 2-celled, each cell binucleate. 7, A mature teliospore, each cell uninucleate. During the maturation of the teliospores, the two nuclei in each cell fuse. 8, A teliospore germinating the spring following its formation. Each cell is sending out a 4-celled promycelium (basidium) each cell of which may produce one basidiospore. The cells of the basidium and the basidiospores are each uninucleate. 9*a* and 9*b*, Basidiospores which will develop into plus and minus mycelia, respectively, which will in turn give rise to plus and minus spermatia. 10, If the basidiospores fall upon a common barberry leaf (10), they germinate as shown in 11, and the germ tube penetrates the leaf epidermis and forms a mycelium within the tissue of the leaf. 12, A barberry leaf (upper surface), showing two groups of spermogonia. 13, Cross sections of two different parts of the same leaf, showing spermogonia in longitudinal section. One of these has developed from a plus mycelium, the other from a minus mycelium. At the tips of hyphae in the spermogonia, spermatia are produced. 14, Nucleus of a spermatium passing into a paraphysis. 15, The lower surface of a barberry leaf bearing the aecia or cluster cups. 16, Cross section of an aecium bearing aeciospores. 17, A binucleate aeciospore. 18, Hypha from a germinating aeciospore entering the stoma of a wheat leaf.

upper side of the leaves, small flask-shaped bodies which break through the epidermis. Somewhat later, clusters of yellowish cups are found on the lower surface of the leaf.

The small flask-shaped bodies are known as **spermagonia.** Within them are produced rod-shaped or oval **spermatia.** The cup-

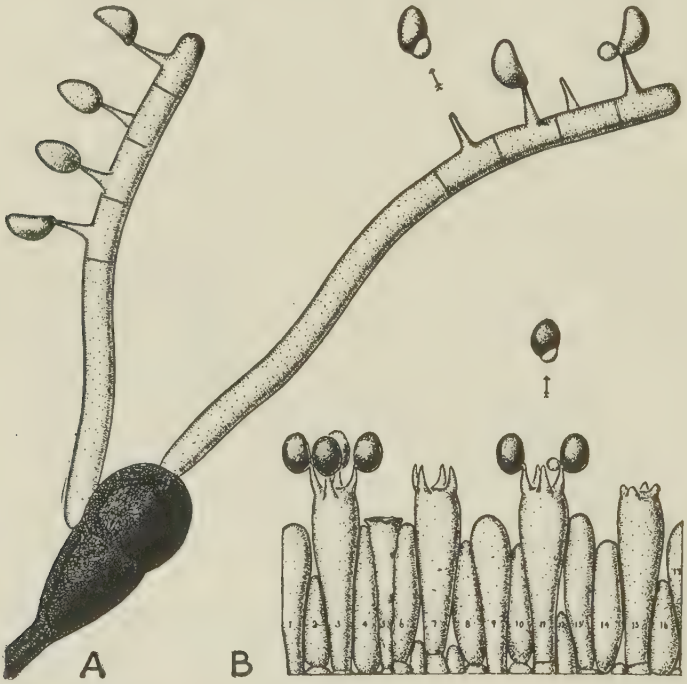


FIG. 203. Spore-discharge in the Uredineae and the Hymenomycetes. *A*, a germinated teliospore of *Puccinia graminis* (from *Avena sativa,* bearing two basidia, one with four ripe spores and the other with spore-discharge going on). *B*, a transverse section through the hymenium of *Psalliota campestris,* showing a basidium with four ripe spores and another basidium with spore-discharge going on. In both *Puccinia graminis* and *Psalliota campestris* a drop of water is excreted from the hilum of each spore just before discharge. Magnification the same both *A* and *B*, 880. (From Buller's *Researches on Fungi.*)

shaped structures are called **cluster-cups** or **aecia.** At maturity these are filled with chains of yellowish one-celled spores, known as **aeciospores.** The aeciospores are scattered by the wind and may infect the grass host. A mycelium, developed within the tissues of the grass plant, gives rise to urediniospores in the manner already described.

For a number of years, the great importance of the barberry in spreading rust has been recognized. Denmark, in 1903, passed a barberry eradication law, and since then almost all bushes have been eradicated from the country. This resulted in almost total elimination of black stem rust in Denmark. In 1918, a vigorous barberry-eradication campaign was initiated in this country by the Office of Cereal Investigations, of the United States Department of Agriculture, cooperating with the thirteen principal wheat-growing states. Already, eradication has progressed so far in certain sections that the beneficial results are noticeable. It is not to be expected that destruction of all plants of those species of barberry which are subject to the disease will eradicate the disease in all localities. In regions where the winters are mild, urediniospores may survive the winter and infect cereals in the spring, thus continuing the disease without the alternate host.

FIG. 204. Leaf of common barberry (*Berberis vulgaris*) showing clusters of aecia on the lower surface. (From Buller's *Researches on Fungi.*)

The Fleshy and Woody Fungi.—This group includes such familiar fungi as mushrooms, puff-balls, and the bracket fungi which are found on trees. A characteristic feature of these forms is the conspicuous spore-producing part, which is the "mushroom," as we ordinarily know it. This structure is not the whole plant but merely a reproductive structure or spore-bearing body (the **sporophore**). The vegetative part of the plant body is the mycelium, which grows saprophytically in soil rich in organic matter or other substratum upon which the sporophores are produced. It consists of extensively branched strands of hyphae which absorb, and use as food, organic material in the substratum. Mushrooms, therefore, are never found except in locations where there is an abundance of organic material, such as decayed leaves and twigs, or manure. It is only after the mycelium has accumulated considerable stores of food that the sporophores are produced.

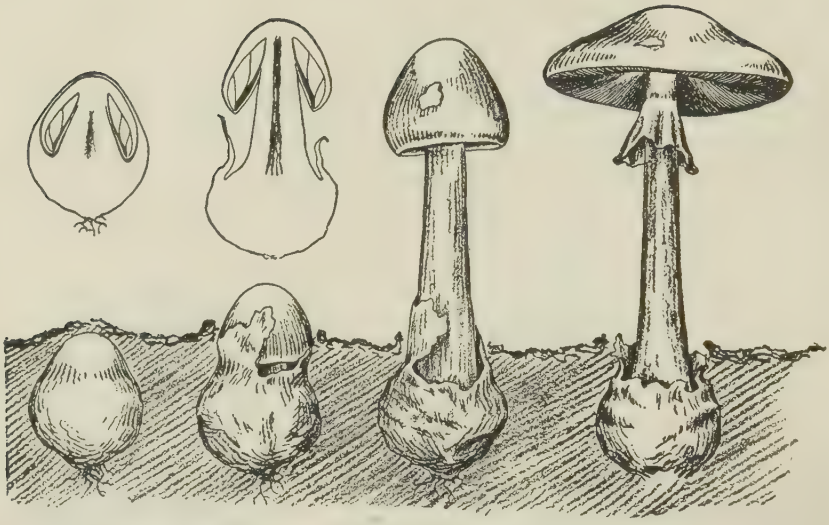


FIG. 205. Stages in the development of a gill fungus (*Amanita*). (After Longyear.)

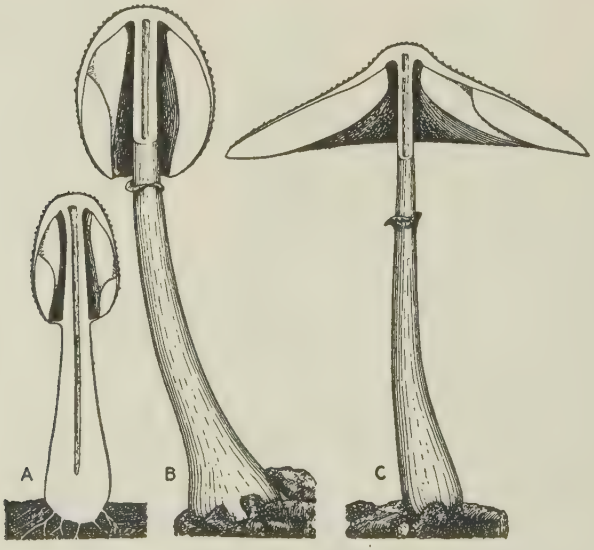


FIG. 206. *Lepiota cepasestipes*. Sections of three fruit-bodies coming up among cinders, Sphagnum, etc., in a hothouse. *A*, in the morning, the gill-chamber still intact. *B*, in the afternoon, the pileus beginning to expand, an annulus left upon the stipe. *C*, at night, the pileus fully expanded and shedding spores. Natural size. (From Buller's *Researches on Fungi*.)

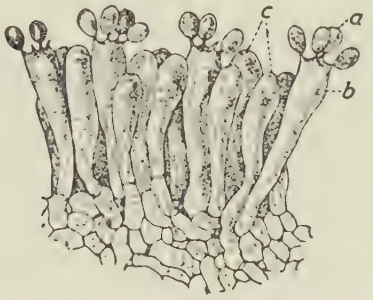


FIG. 207. Small portion of a section through the spore-bearing layer (hymenium) of a mushroom. *a*, basidiospores; *b*, basidium; *c*, paraphyses. (After Longyear, in Colorado Agricultural Experiment Station Bulletin.)

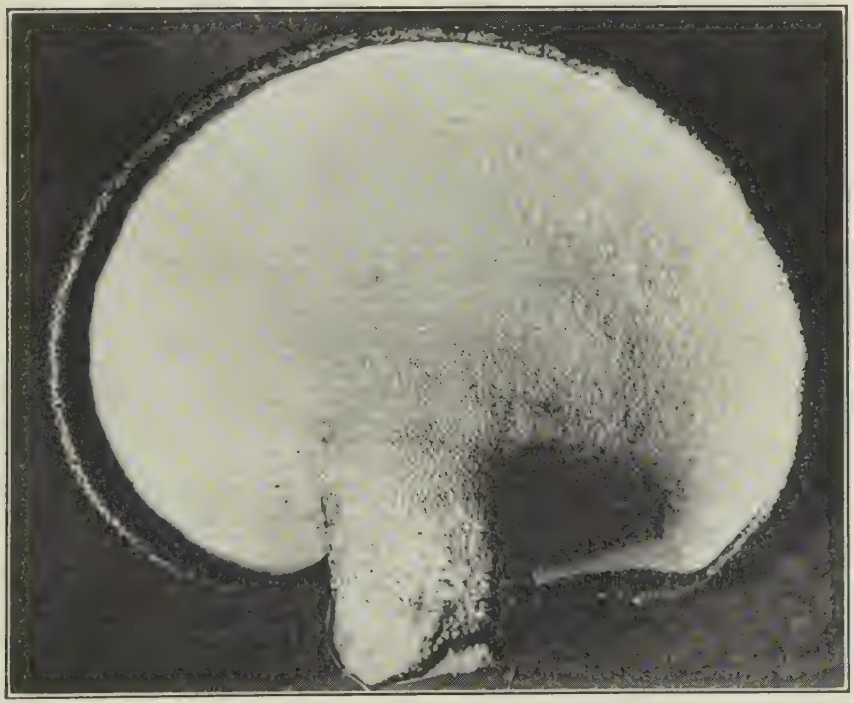


FIG. 208. Under surface of fruit-body of *Polyporus squamosus* nearly full grown, showing the pores of the hymenial tubes and the reticulations on the stipe. The fruit-body was photographed immediately after it was cut; the involution of the edge of the pileus is quite natural. Photographed by R. H. Pickard. One-third natural size. (From Buller's *Researches on Fungi*.)

The mature sporophore, or fruiting body, of a common gill mushroom consists of a stalk or stipe and an umbrella-shaped cap called the pileus. On the under side of this cap there are borne thin plates called gills which radiate from the stalk toward the margin of the pileus and are covered by a surface layer or hymenium which is made up of millions of basidia and sterile hyphae or paraphyses growing out at right angles to the surface of the gill. Generally four spores are produced at the free end of each basidium on four slender projections called sterigmata.

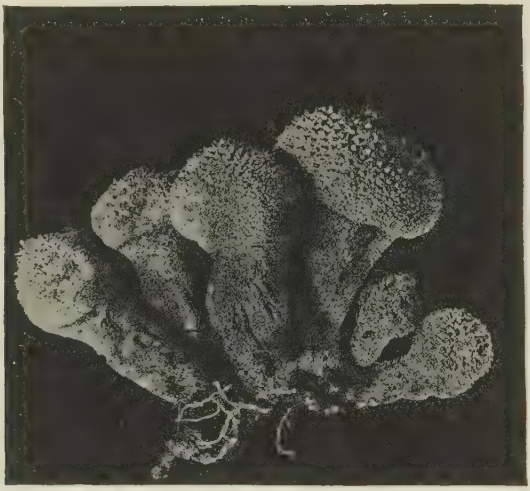


FIG. 209. A cluster of puff balls (*Lycoperdon*). The puff balls are *Basidiomycetes*, which produce their spores within a closed structure. (After Longyear.)

Mushroom "spawn," as sold by seedsmen, usually consists of dried manure and decaying leaves containing the mycelium of mushrooms which have previously grown upon this material. When a mushroom bed is being made, this material is broken up, mixed with earth, and used to start the beds. The partially dried mycelium in the spawn grows rapidly in the moist, warm substratum of the mushroom bed, and later sporophores are formed.

Basidiospores are produced in immense numbers on the hymenium. It has been computed that a single sporophore of *Agaricus campestris*, measuring 8 centimeters in diameter, may liberate as many as 1,800,000,000 spores, and a single fruiting body of *Polyporus squamosus* as many as 11,000,000,000. In the latter case the

spores are liberated at an average rate of at least one million a minute. The spores drop from the sterigmata of the basidia upon which they are borne, and are readily carried far and wide by air currents. Under favorable conditions they germinate and develop a new mycelium, but it has been estimated that in the common mushroom, *Agaricus campestris*, only one spore in twenty billion actually germinates and grows into a mushroom plant.

In the bracket or shelf fungi the hymenium constitutes the lining of many pores formed on the lower side of the sporophores.

Nearly all the deadly poisonous fleshy fungi are species of the genus *Amanita.* This is a group of mushrooms with gills. Some of the species of *Amanita* have white caps, others have bright orange, red, or yellow caps; but in all species the gills are white, and the spores are white. This deadly group is distinguished by the following combination of characters: (1) white spores, (2) "ring" on the stem, and (3) a cup at the base—the so-called "death cup." When a mushroom shows these three features it should be avoided. One should not depend upon the various rules-of-thumb for detecting poisonous mushrooms. The common or cultivated mushroom (*Agaricus campestris*) is a purple-spored form, with pink gills, a broad "ring" on the stem, but no cup at the base.

Basidiomycetes—A Summary.—In this group are included both parasitic and saprophytic fungi. The hyphae are septate and branched. The characteristic feature of the class is the occurrence in the life cycle of a basidium, which produces asexual spores.

CHAPTER XII

EMBRYOPHYTA
BRYOPHYTA

(LIVERWORTS AND MOSSES)

The Bryophyta include plants known as liverworts and mosses. Liverworts are flat green plants, leafless and stemless, growing on moist soil or on rocks near the water. They attain their greatest development in the moist tropics, and in the northern countries where there is ample rainfall. They are in general more strictly confined to very moist habitats than are the mosses. There are some liverworts, however, notably certain forms growing in California and in other regions where there is a long dry season, which are able to survive months of almost complete desiccation. Mosses are a much more conspicuous and important element of the flora than are liverworts. They are not so strictly limited to very moist habitats as are most of the liverworts, and especially in northern countries large areas may be covered with an almost pure growth of mosses, whereas this is seldom true of the liverworts. A few mosses are aquatic, many grow upon soil, and many others grow upon rocks, the bark of trees, and decaying wood.

The algae, which are the ancestors of the mosses and liverworts, are, with few exceptions, aquatic plants. The mosses and liverworts, on the other hand, are the most primitive of the truly terrestrial or land plants, although their adaptation to land conditions is so imperfect that few of them, if any, are able to complete their life cycle without being subjected to a period during which the plant is actually covered with water. The process of fertilization depends upon the presence of free water.

The adoption of a land habitat by the Bryophyta and higher land plants has necessitated certain structural and physiological

adaptations in response to the great difference in the environment of land plants and that of submerged aquatics.

Some of the principal characteristics of the Bryophyta and of higher land plants which are apparently correlated with the differences in environment are:

(*a*) Special structures for the absorption of water and minerals from the soil are developed by all typical land plants—the rhizoids of lower land plants (Bryophyta) and the roots and root hairs of ferns and flowering plants. The rhizoids of the Bryophyta appear, however, not to be very efficient organs for water absorption. Rhizoids and roots differ very markedly in structure.

(*b*) The parts exposed to the air are protected from excessive water loss by the production of a superficial layer of cells (epidermis) having an outer wall which, with its cuticle, is very resistant to the passage of water vapor. It is important that this should not prevent the entrance of the gases needed for photosynthesis and respiration. The epidermis among most land plants, accordingly, has openings through it, called stomata.

(*c*) In all but the smallest land plants there are conductive tissues which provide for relatively rapid transfer of water from the water-absorbing structures to the parts exposed to the dry atmosphere.

(*d*) The more primitive land plants either grow prone upon the ground or, if erect, seldom attain a height of more than a centimeter or two, since they are lacking in mechanical tissues. The higher land plants have developed mechanical tissues and some of them are able to support a stem hundreds of feet high.

(*e*) In the Bryophyta, and in the Pteridophyta as well, fertilization can take place only when the plants which bear the gametes are wet, because the sperms can move only in water. By various means the spores of land plants are adapted to efficient dissemination by air instead of water. Small size and the development of ridges or spines on the outer spore wall are among the principal characteristics favoring wind dissemination. The discharge of spores into the air from elevated structures, such as the long-stalked capsules of the mosses and many liverworts, makes it more likely that they will be carried to some distance by air currents before they fall to the ground.

The single most important point of distinction between the Bryophyta and the Algae is the alternation, in the life cycle of all the bryophytes, of a sexual generation and an asexual generation. This alternation of generations occurs in a few of the Thallophyta but is not characteristic of the group. The asexual or spore-bearing plant is known as the **sporophyte**, and the sexual or gamete-bearing plant is the **gametophyte**.

In all the Bryophyta the gametophyte is "the plant," that is to say, the gametophyte is the conspicuous and independent plant, which alone is able to absorb water and soil solutes and to which the function of food manufacture is entirely or largely restricted. The sporophyte is smaller than the gametophyte and is permanently attached to, and grows more or less parasitically upon the gametophyte, never establishing direct connections with the soil. It is among the Bryophyta that the gametophyte reaches its highest development among plants. The gametophyte at its best, however, never becomes an efficient land plant.

Sexual reproduction is heterogamous (by means of the fusion of two kinds of gametes—eggs and sperms), as in all plants above the Thallophyta. The female **gametangium** (egg-producing organ), called the **archegonium** in the Bryophyta and Pteridophyta, does not consist of a single cell, the protoplasm of which forms one or several female gametes (egg cells) as does the oogonium of the Thallophyta. Instead it is a **multicellular** flask-shaped **organ**, and the single egg cell is surrounded by a wall made up of **many cells**, instead of being surrounded by a **cell wall only**, as in the Thallophyta.

The male gametangia or antheridia (sperm-producing organs) of the Bryophyta are also distinctly different from those of the Thallophyta, the wall surrounding the sperms produced by one antheridium being made up of a **layer of cells** instead of consisting, as in the Thallophyta, merely **of a cell wall**. This applies as well to the Pteridophyta as to the Bryophyta.

Fertilization cannot take place unless the plants are wet, for it must be possible for the sperms, which are ciliated protoplasts, to swim to the archegonia.

The asexual spores of the Bryophyta (and the Pteridophyta and Spermatophyta as well) are formed in groups of four (tetrads), each tetrad being formed as the result of two divisions of a single cell (the spore mother cell).

No true roots are formed in this division of the plant kingdom, but the sexual or gametophyte plants produce organs called rhizoids which perform the functions carried on by the roots of ferns and seed-bearing plants.

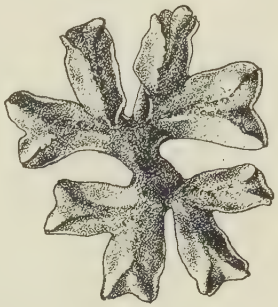


FIG. 210. Thallus of a terrestrial species of *Riccia*. (Magnified about 8×.)

The Bryophyta are divided into two classes, the Hepaticae, or liverworts, and the Musci, or mosses. We shall describe the structure and reproduction of a number of representatives.

Riccia.—*Riccia* is a type which illustrates the simplest sporophyte found in the liverworts, although the gametophyte is not so simple as are those of some other members of this class.

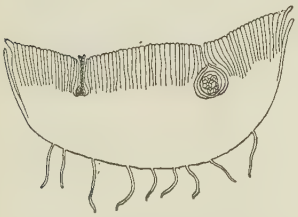


FIG. 211. Cross section, somewhat diagrammatic, of the thallus (gametophyte) of *Riccia* showing on the left an unfertilized archegonium sunk in a deep depression. On the right is a sporophyte within the enlarged venter of an archegonium from the fertilized egg cell of which the sporophyte developed. The chlorophyll-bearing tissue of the upper portion of the thallus is also shown as well as the colorless tissue of the lower part of the thallus, and the rhizoids. (Magnification about 30×.)

The gametophyte consists of a small, flattened, freely branching thallus, with a depression along the middle line of the upper side. From the under side of the thallus numerous rhizoids grow out. They are very similar to root hairs and are merely long tubular extensions of certain of the cells of the lower surface of the thallus. They function as organs of attachment and absorption. The upper portion of the thallus consists of chlorophyll-bearing tissue where food manufacture is carried on, and the lower portion of colorless tissue which serves for food and water storage.

The antheridia and archegonia are sunk in depressions in the thallus, opening out into the median furrow. In *Riccia*, antheridia and

archegonia are borne on the same thallus, but in many species of liverworts they occur on different plants. The biciliate sperms are formed in great numbers in pear-shaped antheridia, each of which consists of a single layer of sterile cells enclosing the sperm cells. The archegonium consists of an enlarged basal portion, the **venter**, and a slender elongated tubular portion called the **neck**. The cavity of the neck and venter contains a single row of cells, the lowest one, which is the egg cell or female gamete, being the largest and occupying most of the cavity of the venter. When the plants are wet the mature antheridia open as the result of the absorption of water by the gelatinous cell walls and their consequent swelling. The

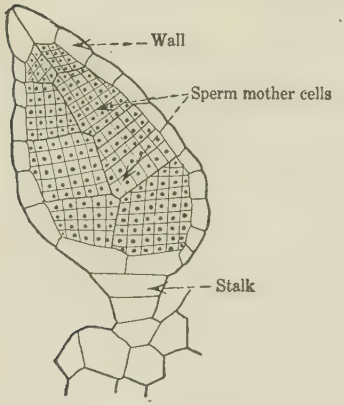


FIG. 212. An antheridium of *Riccia* in section.

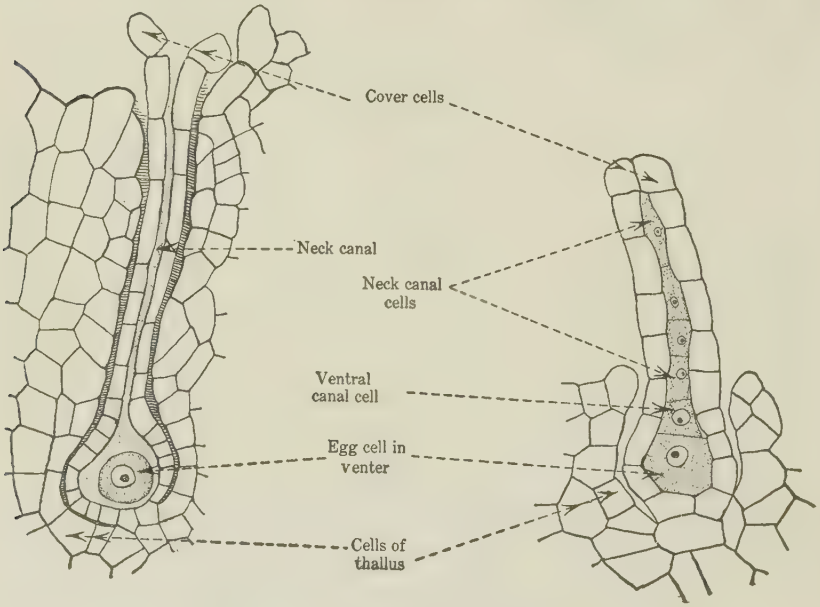


FIG. 213. Archegonia of *Riccia* surrounded by the tissue of the thallus. To the right, an almost mature archegonium. To the left, an archegonium ready for fertilization. (Drawn from preparations of D. H. Campbell.)

motile sperms are thus freed and swim to the opening of the neck of

the archegonia, the neck cells of which have degenerated into a mucilaginous material and dissolved, leaving a free passage to the egg cell.

The formation of the zygote by the fusion of one sperm with each egg cell marks the beginning of the sporophyte or asexual generation. The sperm and egg cell and all the other gametophyte cells have the haploid (n) number of chromosomes, but all the cells of this generation have the diploid ($2n$) chromosome number. The zygote, by repeated divisions, gives rise to a spherical structure (the sporophyte) many times the size of the zygote. This structure consists of a wall made up of a single layer of flattened sterile cells and, within this wall, a number of free spherical cells each of which divides up into a tetrad of four spores. The spores are freed by the decay or shriveling of the tissue of the gametophyte, and on germination form new gametophyte plants. The first of the two nuclear divisions by which each spore mother cell produces four spores is a reduction division by which the chromosome number is reduced to the haploid number.

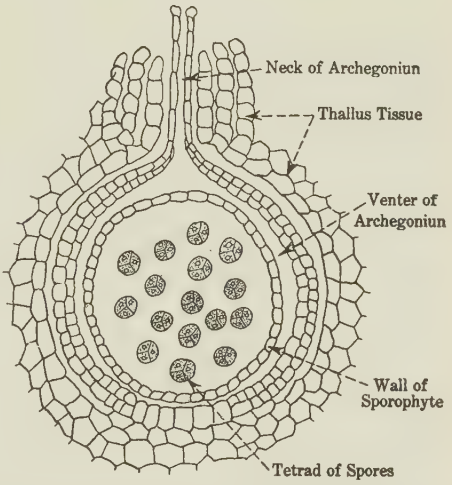


FIG. 214. Diagrammatic figure showing, in a section cut at right angles to the surface of the thallus, the mature sporophyte and enlarged archegonium of *Riccia*.

Marchantia.—In *Marchantia,* the gametophyte, like that of *Riccia,* is a branched thallus, bearing rhizoids on the lower side. *Marchantia,* unlike *Riccia,* is dioecious, that is, the gametangia or sex organs (archegonia and antheridia) are borne on different thalli (gametophytes). Moreover, the gametangia, instead of being buried in depressions in the thallus, as in *Riccia,* are produced on special erect thallus branches, the **antheridial receptacle** or disk, and the **archegonial receptacle,** each supported on a slender

stalk. Numerous antheridia or archegonia are produced on each receptacle.

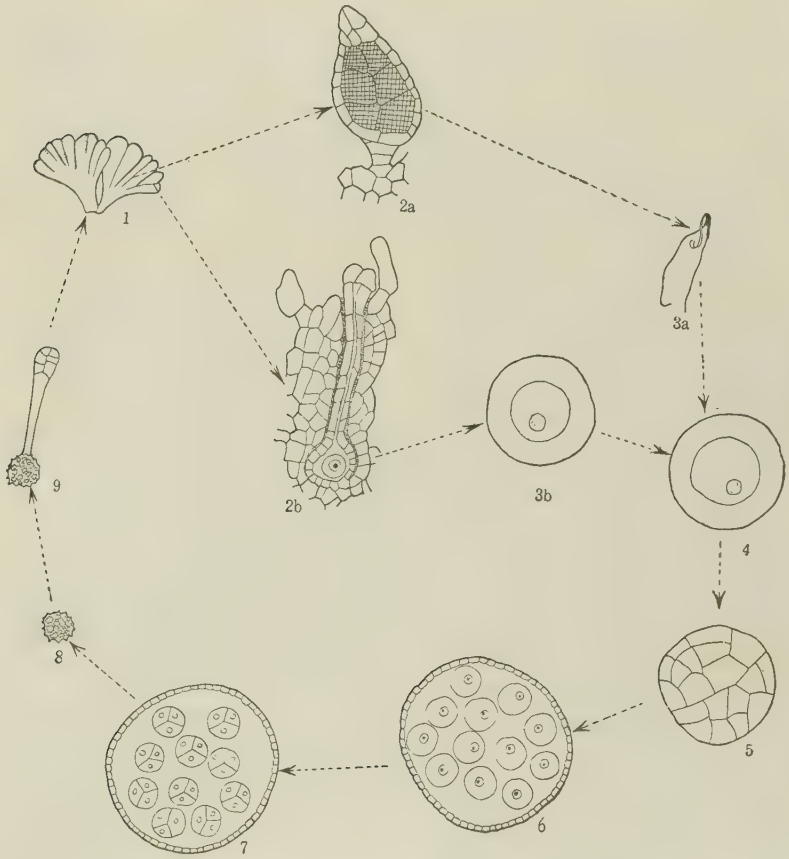


FIG. 215. Diagram showing the life cycle of *Riccia*. 1, the gametophyte thallus (monoecious). 2*a*, an antheridium. 2*b*, an archegonium ready to open and permit the entrance of sperms (both antheridia and archegonia are sunk in the tissue of the thallus.) 3*a*, a single sperm. 3*b*, an egg cell. 4, the fertilized egg cell or zygote. 5, an embryo sporophyte resulting from repeated divisions of the zygote. 6, the sporophyte with contained spore mother cells. 7, tetrads of spores each such group of four resulting from two divisions (the first a reduction division) of a spore mother cell. 8, a single ripe spore. 9, a very young gametophyte plant developed from a spore. Note that stages 4-6 and the wall cells in 7 belong to the sporophyte generation, the other structures to the gametophyte.

In *Marchantia* the process of fertilization and the early stages of the development of the embryo sporophyte from the zygote (fertilized egg cell) are very similar to those of *Riccia*.

The sporophyte of *Marchantia* is larger than that of *Riccia* and more complex. It consists of a foot which acts as an organ for attachment to the gametophyte and for absorption of food from it, a stalk and a capsule within which the spores are formed. Much of the sporophyte of *Marchantia* consists of sterile cells, i.e., there is relatively much less sporogenous tissue in the sporophyte of *Marchantia* than in *Riccia*. Even within the capsule some of the

FIG. 216. Thalli (male) of *Marchantia* as seen in natural habitat. A number of antheridial branches may be seen.

cells instead of forming spores develop into peculiar sterile cells called elaters, which aid in spore dissemination.

In *Marchantia* there is rather effective provision for the distribution of spores, whereas such provision is lacking in *Riccia*. In the former plant, the facts that the sporophyte is not buried in the gametophyte tissue, and that it is attached in a pendent position to the under side of the stalked archegonial branch, as well as the presence of a stalk and the presence of elaters among the spores, all favor widespread dissemination of spores. In *Riccia*, on the other

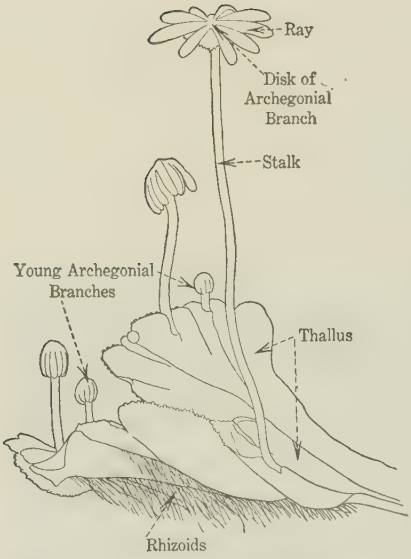


FIG. 217. A portion of the female gametophyte of *Marchantia*, showing archegonial receptacles.

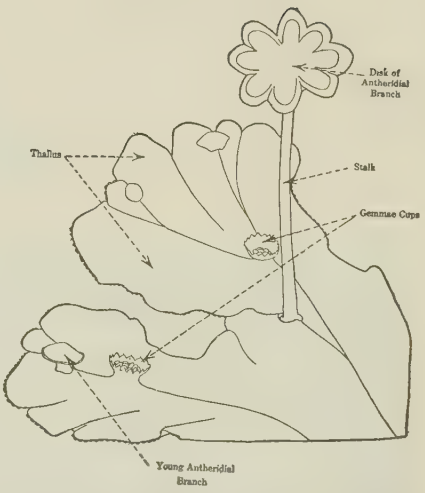


FIG. 218. A portion of the male gametophyte of *Marchantia*, showing antheridial branches and gemmae cups. The latter are also sometimes produced on the female gametophyte.

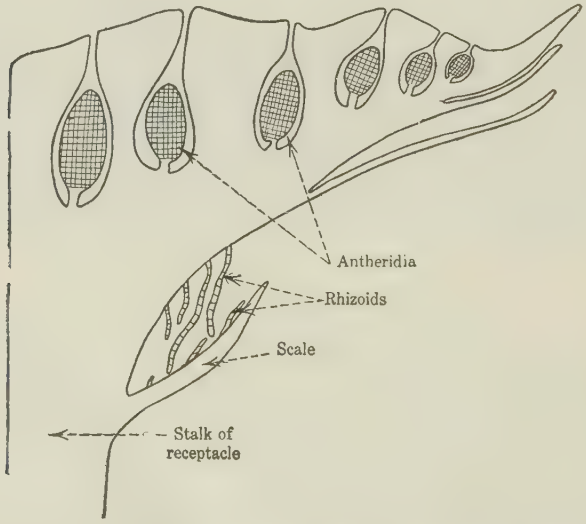


FIG. 219. Diagram of half of an antheridial disk of *Marchantia*, showing the position of the antheridia. The antheridia are essentially the same in structure as those of *Riccia* as shown in Fig. 212 and have a wall one cell layer thick, not shown in this diagram, within which are great numbers of sperm-producing cells.

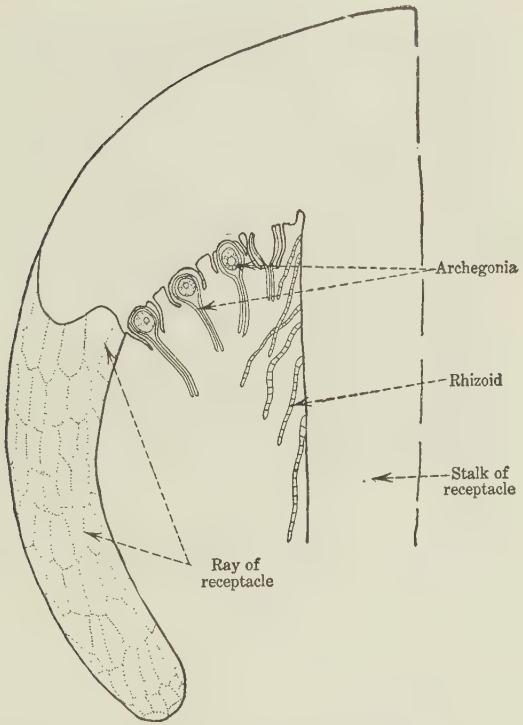


FIG. 220. Diagram of half of an archegonial receptacle of *Marchantia*, showing the position of the archegonia.

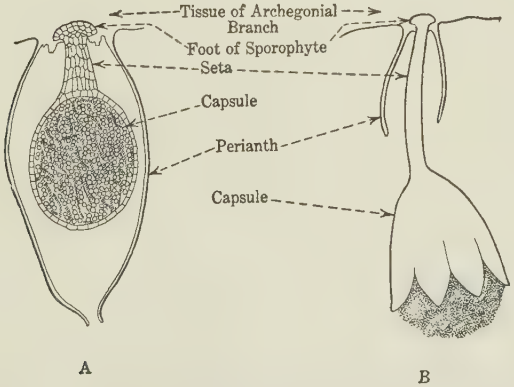


FIG. 221. *Marchantia*. *A*, median longitudinal section of a sporophyte. *B*, sporophyte, with capsule dehiscing. In both figures, a portion of gametophytic tissue is shown.

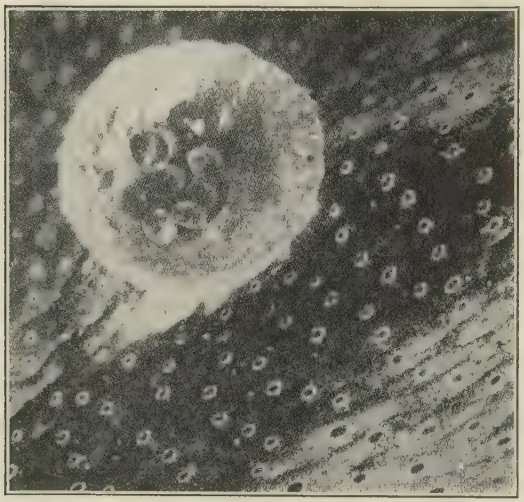


FIG. 222. Photomicrograph of a portion of the upper surface of the thallus of *Marchantia*, showing a gemma cup in which may be seen a number of gemmae. Notice also the conspicuous openings (stomata) through the epidermis.

hand, the spores, buried within the gametophyte, escape only by the distintegration of the tissue of the latter.

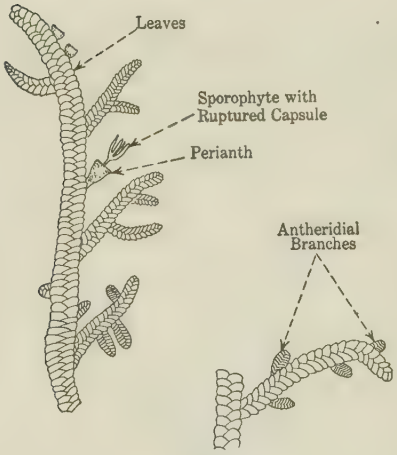


FIG. 223. A leafy liverwort (*Porella*). At left, a portion of a female gametophyte; at right, a portion of a male gametophyte.

In most liverworts the sporophyte is parasitic upon the gametophyte, securing from it all its water and food. The gametophyte of many liverworts is leafy, rather than thallose, as in *Riccia* and *Marchantia*.

Marchantia and a number of other related liverworts are capable of multiplying themselves vegetatively, that is, without the formation of sex organs. On the upper side of the thallus, there occur small cups, within each of which are produced small disk-like bodies, known as **gemmae**, each consisting of a number of cells, mostly green. The gemmae

separate readily from the base of the cup. When thus separated from the thallus a gemma may grow into a new gametophyte thallus.

Although mention has been made here of but two liverworts, *Riccia* and *Marchantia*, both of which are fleshy, thallose forms,

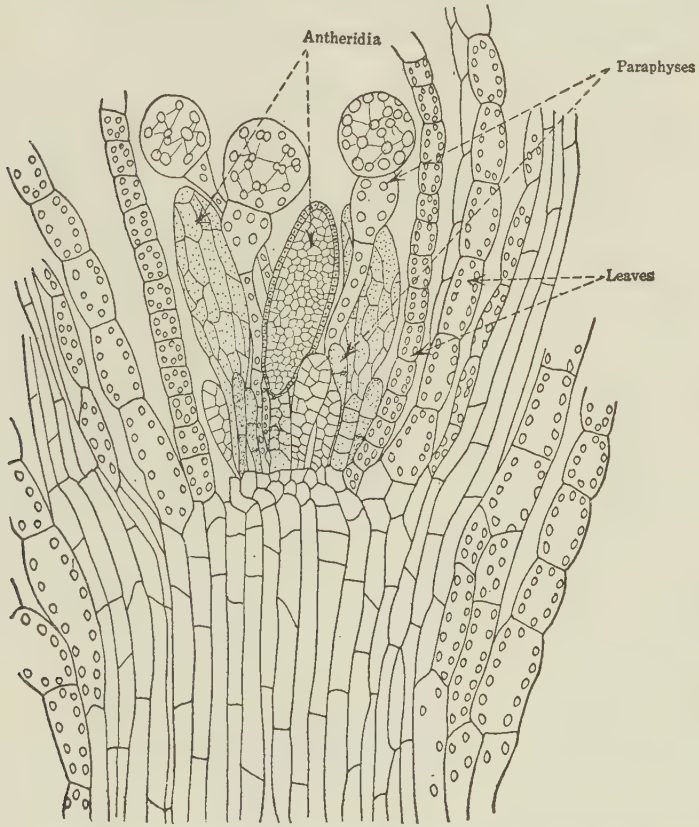


FIG. 224. *Funaria hygrometrica*. Longitudinal section of tip of a male gametophore showing antheridia and paraphyses. (Redrawn from Sachs.)

many species of liverworts, in fact most species, are leafy like *Porella*, but their reproduction is not essentially unlike that of the thallose forms.

THE MOSSES (MUSCI)

The common moss, *Funaria*, may be taken to illustrate the principal features of the structure and development of the plants of this group. The "moss plant" as we know it is the haploid phase

of the plant. It consists of a small stem bearing simple spirally arranged leaves. Within the stem and in the midribs of the leaf there are somewhat elongated cells which are apparently adapted for water conduction, but there is no well-differentiated vascular system. From the lower parts of the stem arise filaments of cells called **rhizoids**, which perform the functions of roots.

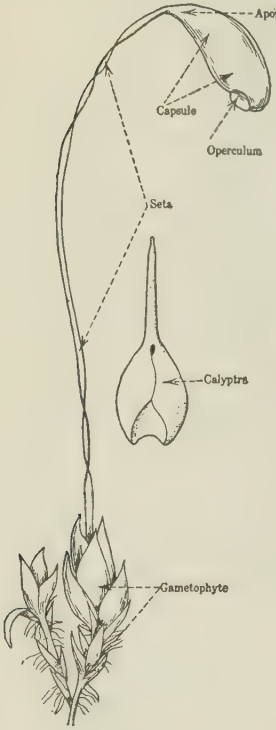


Fig. 225.

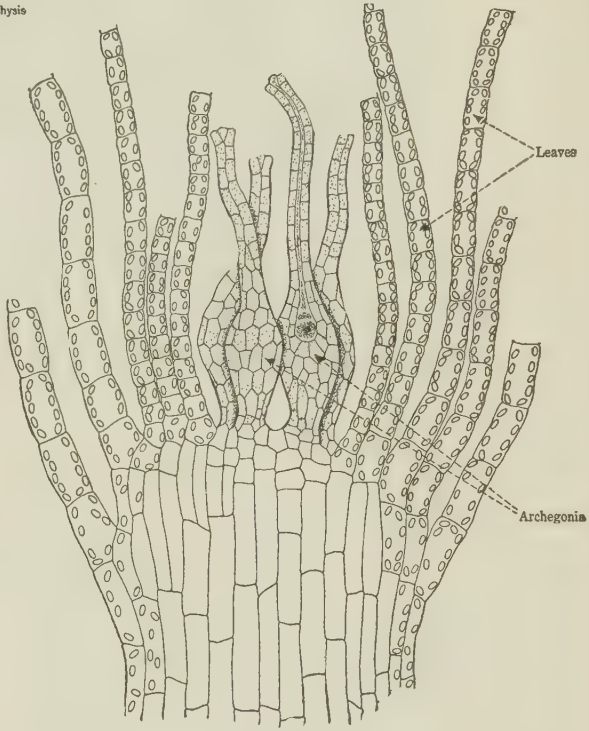


Fig. 226.

Fig. 225. Portion of a gametophyte and attached sporophyte of a common moss, *Funaria hygrometrica.*

Fig. 226. *Funaria hygrometrica.* Longitudinal section of tip of a female gametophore, showing archegonia. (Redrawn from Sachs.)

The gametangia (archegonia and antheridia) are produced in groups at the ends of the leafy shoots. Many sterile hairs, known as paraphyses, occur among the antheridia and archegonia. The antheridia and archegonia of *Funaria* are essentially the same in structure as those of the liverworts. As in the liverworts, the antheridia and archegonia can open and fertilization can take place only when the plants are wet.

The sporophyte or $2n$ or diploid phase of the plant which develops from the zygote is a larger and more complex organ than the sporophyte of the liverwort's structure, in which the spore-producing tissue is much reduced and tissues for photosynthesis and elaborate provision for spore dissemination are present. The sporophyte con-

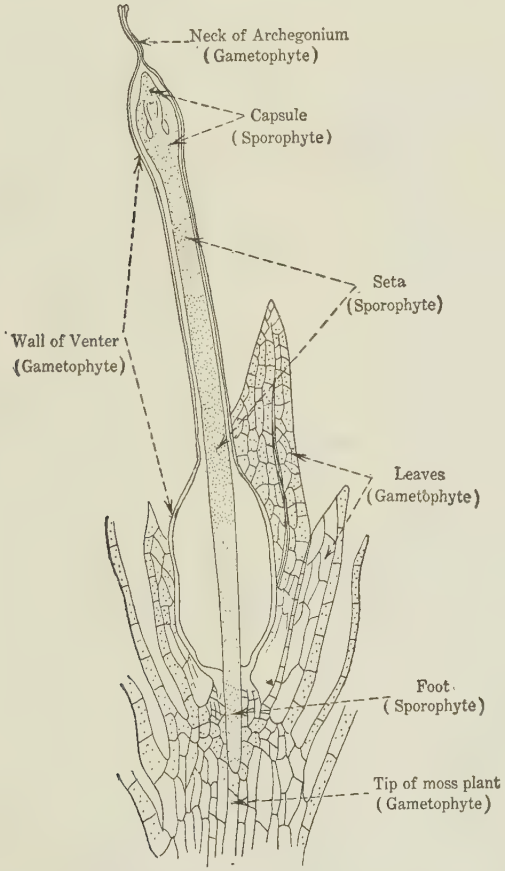


FIG. 227. Tip of a female gametophyte branch and advanced sporophyte as seen in longitudinal section (semi-diagrammatic). The shaded structure is the sporophyte. (Adapted from Sachs.)

sists of (*a*) the **foot**, which penetrates the tip of the stem of the gametophore and serves as an organ of attachment and absorption, (*b*) the **stalk** or **seta**, and (*c*) the **capsule**, a complex structure within which the tetrads of spores are produced but which is mostly made up of sterile tissue. In the formation of these spores the

reduction division takes place so that the spores have the haploid number of chromosomes. In spite of its relative complexity the sporophyte's possibilities of development are limited by reason of the fact that it is restricted, in the quantity of water and salts it can secure, by the limited ability of the gametophyte for absorption and conduction. The sporophyte must secure all its water and soil solutes through the foot, which absorbs them from the gametophyte stem in which it is embedded.

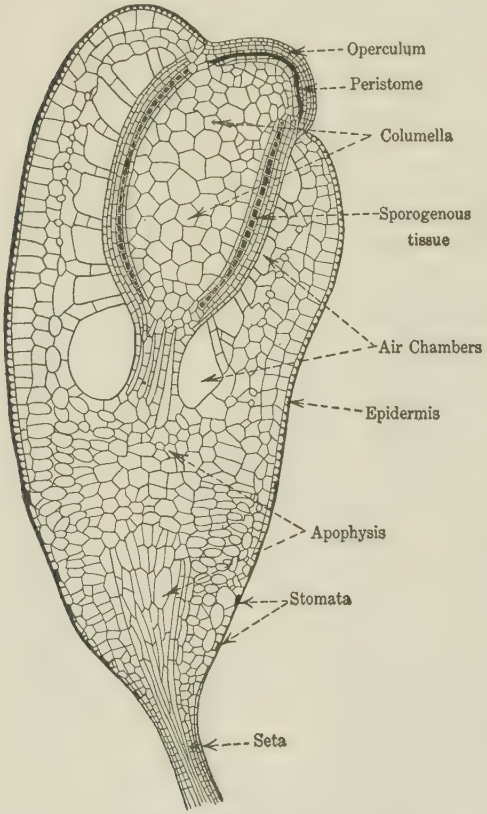


Fig. 228. Longitudinal section of the capsule of the sporophyte of *Funaria hygrometrica.*

The mature capsule of the moss sporophyte is a structure of considerable complexity. Over the top is a cap of tissue, the **operculum.** When the capsule is mature and begins to dry up, the operculum becomes loosened and falls off. Before it falls, a double fringe of long triangular teeth, the **peristome,** is formed by radial splitting of several layers of tissue just below the operculum. By the time the spores are ripe and the operculum has been lost, most of the thin-walled cells within the capsule collapse, leaving a cavity which is filled with a loose mass of spores. The peristome teeth are rough by reason of the attached fragments of cell walls, and they are highly hygroscopic. When they are wet or the atmospheric humidity is very high, the peristome teeth bend inward and reach into the cavity of the capsule. When they become dry they straighten out and lift out some of the spores which then are disseminated by air movements.

The spores, which are produced in great numbers, are very small and well adapted to dispersal by wind. On germination, they give rise to the haploid phase of the plant but not directly to the leafy gametophyte. First there is formed a green filament made up of cells placed end to end as in many of the green algae. This

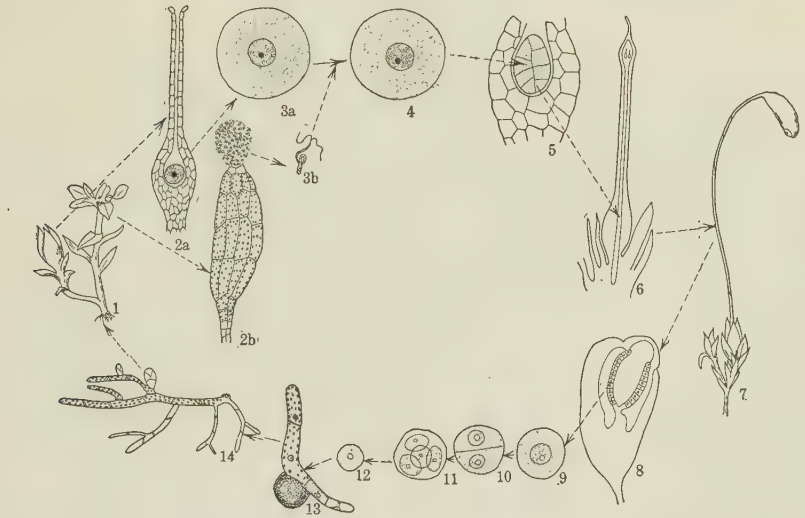


FIG. 229. Diagram showing the life cycle of a typical moss (*Funaria*). 1, the leafy gametophyte plant (gametophore), showing an antheridial and an archegonial branch. 2*a* and 2*b*, an archegonium and an antheridium with mature egg and sperm. 3*a* and 3*b*, an egg and a sperm. 4, the zygote resulting from their fusion. 5, a young embryo sporophyte within the venter of the archegonium. 6, sporophyte in advanced stage of development, attached to the gametophyte and surrounded by the enlarged archegonium. 7, mature sporophyte attached to the gametophyte. 8, section of the sporophyte capsule showing the location of the spore mother cells. 9, spore mother cell. 10, two cells resulting from reduction division of the spore mother cell. 11, tetrad of spores resulting from division of the two cells. 12, a single spore. 13, germinating spore showing protonemal thread and rhizoid. 14, young gametophyte plant showing the buds which develop into leafy shoots of the gametophyte. The stages from 4 to 9 belong to the sporophyte generation. Those from 10 to 3 to the gametophyte generation.

filamentous stage of the gametophyte which branches freely is called the protonema; by means of numerous conspicuous chloroplasts, it carries on photosynthesis which makes possible its growth. Special branches which arise from the protonema produce erect stems bearing rhizoids at the lower end and simple leaves above. This is the stage of the gametophyte which we usually think of as "the moss plant."

CHAPTER XIII

EMBRYOPHYTA
PTERIDOPHYTA

(FERNS AND FERN ALLIES)

The ferns and their allies constitute a large group of plants which have certain resemblances to the liverworts and mosses on the one hand, and to the seed plants on the other. They resemble the Bryophyta in the following important particulars: (1) They produce ciliated male gametes; (2) they require water in order that fertilization may take place; and (3) they have sex organs which are essentially of the same structure as those of the liverworts and mosses. They resemble the Spermatophyta in that the spore-bearing plants (sporophytes) all have roots and can therefore live independent of the gamete-bearing plants (gametophytes), and in that they possess well-developed vascular (conducting) tissue.

We are familiar with the general appearance and habit of the true ferns—those of shady forests, and those so common in conservatories and homes. Plants known as the "fern allies" include the club mosses and scouring rushes. Some of the creeping club mosses are known as "ground pine." The scouring rushes, also known as "horsetails," belonging to the single genus *Equisetum,* have conspicuously jointed hollow stems and small scale leaves. The harsh texture of scouring rushes is due to the heavy impregnation of the outer tissue with silica. Because of the siliceous deposit the plants were formerly used for cleaning and polishing metal utensils and given the name of "scouring rush." These plants grow for the most part in moist locations and are frequently found as weeds in poorly drained agricultural land.

There is fossil evidence that some among the various species of *Equisetum* and related genera were of great size and formerly constituted a much more important element in the earth's flora than do the equisetums of today.

THE TRUE FERNS

The true ferns are widely distributed over the surface of the earth. They flourish most luxuriantly in moist, shady habitats, but there are some species which grow in very dry situations. Ferns attain their greatest size in the tropics, where certain tree ferns

FIG. 230—Sporophyte of Christmas fern (*Polystichum*), showing the horizontal rhizome bearing at the tip young coiled leaves, the expanded leaves of the previous season, each with a stalk or stipe prolonged to form the rachis from which pinnae (leaflets) arise laterally, and the fibrous roots which arise from the lower side of the rhizome. The older parts of the stem are covered with the petioles of dead leaves. (After Curtis.)

grow to a height of 30 feet or more. The stems of such tree ferns are erect, woody, and unbranched, and each bears at its tip a cluster of compound leaves, the fern fronds. Most common ferns, however, have most of their stem system underground.

In following through the life history of a true fern, we will select

the common fern (*Polypodium*) as being typical of the group. The familiar fern plant, as we know it, with its roots, stem, and leaves (fronds), is the asexual or spore-bearing diploid phase or generation commonly spoken of as the sporophyte. In *Polypodium*, as in most common ferns of temperate regions, the stem is subterranean and generally grows horizontally a few inches beneath the surface of the ground. It usually branches sparingly, and at the free ends are the buds which are protected, as a rule, by a dense growth of scales and epidermal hairs. Increase in length of the rhizomes continues from year to year by growth from these terminal buds. Hence, the rhizome is perennial. Each year new adventitious roots arise from the lower side of the rhizome and new leaves from its upper side. The leaves generally die at the close of each growing season. Examination of the older portions of the stem shows them to be covered by the bases of the petioles of dead fronds. By the death of older parts of the rhizome, branches become disconnected from the main rhizome and continue their development as separate new plants. In this way vegetative reproduction is accomplished. Ferns are propagated commercially chiefly by division of the rhizome.

FIG. 231. The sporophyte of horsetail (*Equisetum arvense*) showing green vegetative shoots (left) and spore-bearing shoots (right) and the rhizomes from which these aerial shoots arise. Note the whorls of scale leaves, and on the vegetative shoot the whorls of green branches.

The stem of ferns is much more complex in structure than any organ found in the Bryophyta. Its outstanding structural feature is a water- and food-conducting system (vascular system).

The roots are small and fibrous, and, except for the primary

root, which soon dies, all roots are adventitious and arise from the lower side of the stem.

The frond of *Polypodium* and most common ferns consists of a

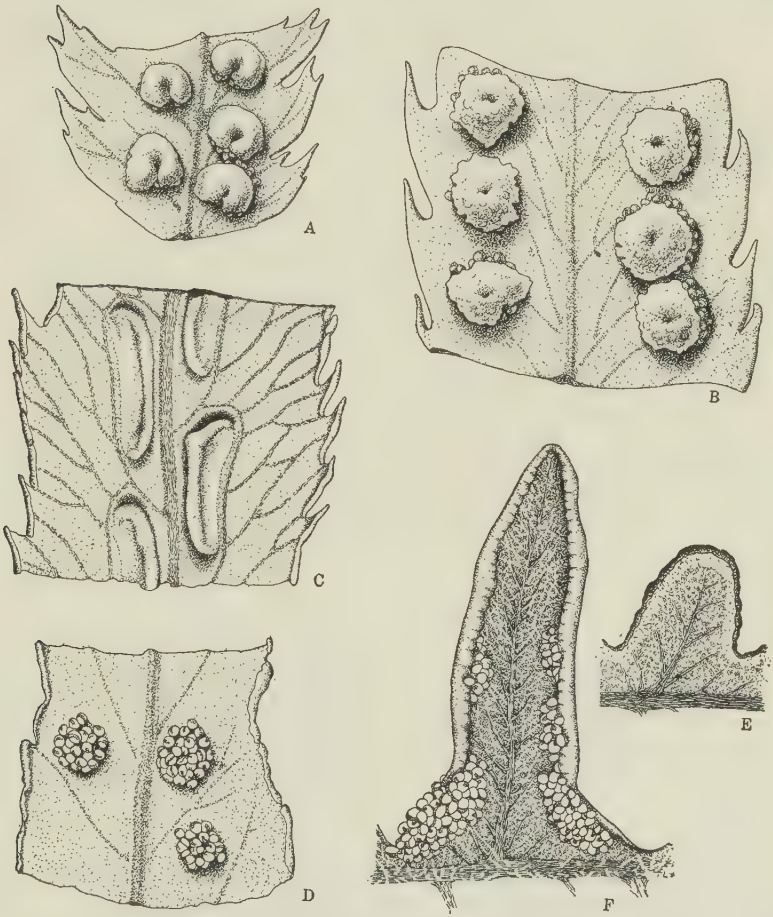


FIG. 232. Sori and indusia of various types. *A*, sori of *Dryopteris* with kidney-shaped indusia. *B*, shield-shaped indusia of *Polystichum* sori. *C*, linear indusia covering the sunken sori of *Woodwardia*. *D*, naked sori of *Polypodium* which are without indusia. *E* and *F*, a young and an older pinnule of *Pteris* showing the false indusium (inrolled margin of the leaf) characteristic of *Pteris* and several related genera.

stalk or stipe, which is prolonged to form the rachis, from which arise laterally a number of pinnae (leaflets). Leaf primordia may be observed as small swellings near the growing point of the rhizome. These leaf primordia grow very slowly, in fact in some species it is

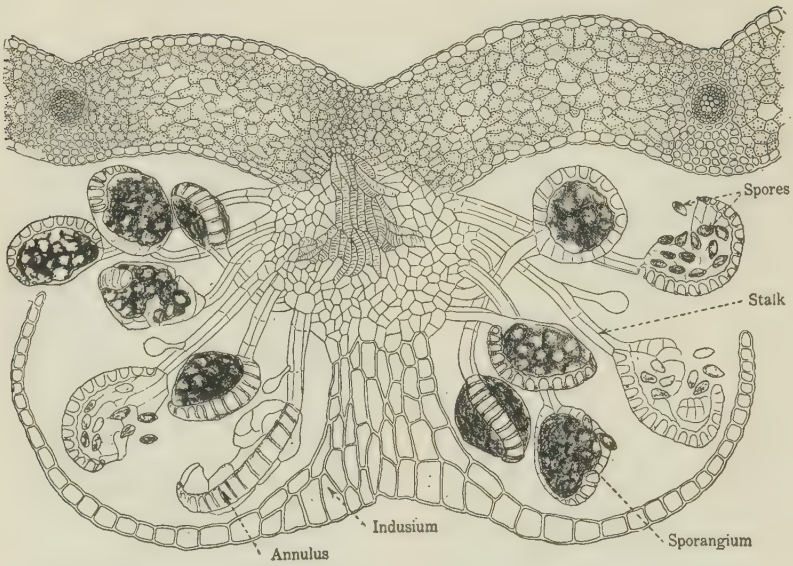


FIG. 233. Cross section of fern leaf, through a sorus. Note the epidermal layers, chlorenchyma and veins of the leaf, as in higher plants. Different views of the sporangia are shown. (Redrawn from Kny.)

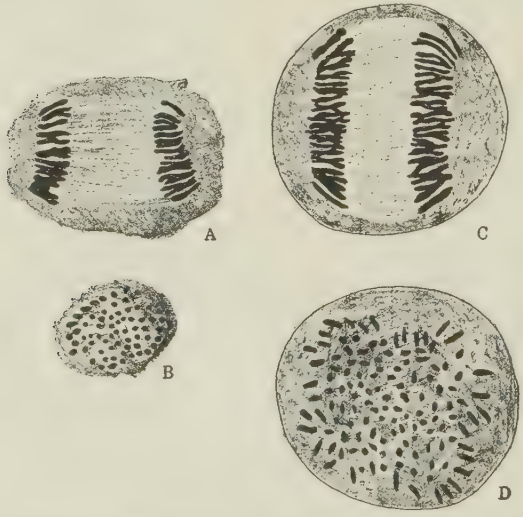


FIG. 234. Nuclei from the gametophyte (*A* and *B*) and of the sporophyte (*C* and *D*), of *Nephrodium* during mitosis, showing 64 and 128 chromosomes respectively. (Redrawn from Yamanouchi.)

not until the spring of the third year following their origin that the leaves appear above the ground.

Fern leaves continue to grow at the apex until their full size is reached. In this particular they differ from the leaves of seed plants, in which growth is apical only in very young leaves. They are of much the same structure as those of seed plants, having an upper and lower epidermis, chlorenchyma tissue, vascular bundles, and stomata. The stomata are usually confined to the under surface. The chlorenchyma is generally not sharply differentiated into palisade and spongy parenchyma.

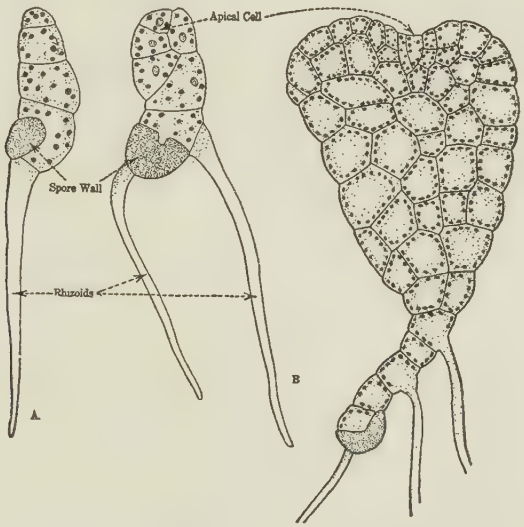


FIG. 235. Early stages in the development of the gametophyte of *Polypodium*. (See explanation in text.)

The spore-cases (**sporangia**) are in clusters on the under side of the frond. These clusters appear as brownish "dots." The groups or clusters of sporangia are called **sori** (singular, **sorus**). In many species, but not in *Polypodium*, there is a membranous covering (**indusium**) over each sorus. Fronds which bear spores are spoken of as **sporophylls**. In *Polypodium* all the fronds are sporophylls; that is to say, the functions of photosynthesis and spore production are combined in all the leaves and there is no differentiation into sporophylls and vegetative leaves. In some ferns, however, the sporangia are definitely limited to a certain few fronds which may

be quite unlike the other leaves. In *Polypodium* each sporangium consists of a stalk and capsule.

The wall of the capsule is composed of a single layer of cells, which are thin-walled except for the annulus, a row of cells extending from the stalk over the top of the capsule and part way down

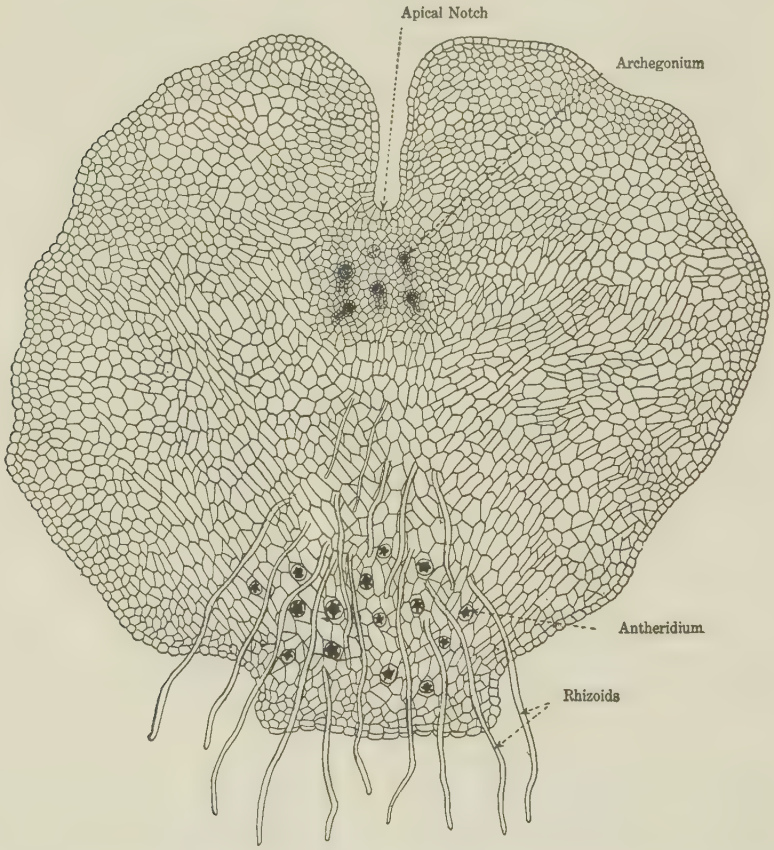


FIG. 236. Mature gametophyte (prothallium) of fern, as seen from the ventral surface.

the other side. The inner and radial walls of the cells composing the annulus are much thickened; the outer walls are relatively thin. Between the end of the annulus and the stalk are a few thin-walled cells, two of which, the lip cells, are narrow and radially elongated. At maturity the sporangium wall splits between these two lip cells.

The spores are formed in tetrads (groups of four) as in the Bryophyta. When the spores are formed, one of the two cell divisions which produces each group of four spores is a reduction division, so that the spores have the haploid (n) chromosome number. The spores of *Polypodium* are all alike, and this genus is therefore said to be **homosporous,** in contrast with those pteridophytes (*Selaginella* and others) which produce two kinds of spores differing in size and other respects and which are said to be **heterosporous.**

FIG. 237. Mature archegonium of a true fern ready for fertilization.

As the sporangium becomes progressively drier, the annulus begins slowly to straighten out, and as it does so the weak lip cells and the thin side walls of the sporangium are torn. Finally, the annulus may almost double back upon itself, pulling with it a mass of ripe spores. Suddenly, with a snap, the annulus returns to its original position, at the same time dispersing the spores. In their dry condition the spores are easily disseminated by wind.

A spore on germination forms a gametophyte, or **prothallium,** which is a flat, green, heart-shaped plate of cells a few millimeters in diameter, and even simpler in structure than are the gametophytes of the bryophytes. All the cells of the prothallium have the haploid chromosome number. Fern prothallia often may be observed on the moist soil beneath fern plants. In *Polypodium* and in most other ferns, each prothallium bears both antheridia and archegonia; that is to say, most ferns are monoecious. Some species, however, have the male and female gametangia on different gametophytes, that is, are dioecious. The gametangia are borne on the under surface of the prothallium, the archegonia near the notch of the thallus, the antheridia scattered among the rhizoids. The archegonia and anteridia, although differing from those of Bryophyta in certain particulars, are essentially similar to them.

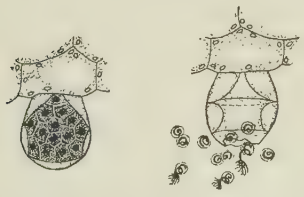


FIG. 238. Antheridia of a true fern, one showing escape of sperms after rupture of antheridium wall. (After Atkinson.)

The sperms are released from the antheridia in the presence of

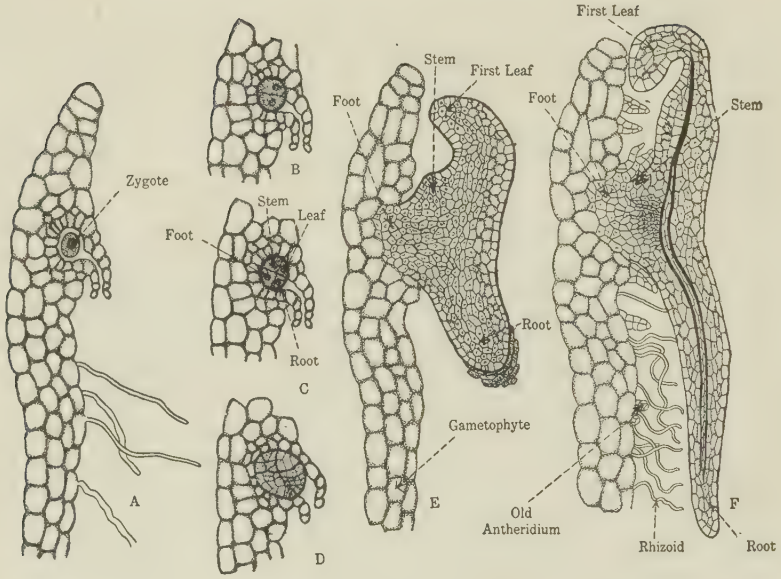


FIG. 239. Stages in the development of the fern sporophyte.

water. They swim to the neck of the archegonium and move down the neck-canal to the egg. At fertilization, the number of chromosomes is doubled so that the zygote (fertilized egg) and all of the cells of the sporophyte plant which develops from the zygote have the diploid number.

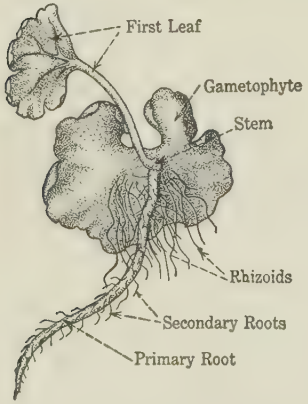


FIG. 240. Fern sporophyte after its root has entered the soil and its first leaf has begun to carry on photosyntheses but before the death of the gametophyte.

After fertilization the zygote begins its development into "the fern plant" (sporophyte). The embryo of the young sporophyte develops the following four primary organs:

1. The foot, which is a mass of small cells embedded in the tissue of the prothallium (gametophyte), and which absorbs food and water for the young embryo from the gametophyte.

2. The root, which grows downward and pushes its way into the soil.

3. The primary leaf, which, though little resembling the permanent leaves, is the first photosynthetic organ of the sporophyte.

4. The stem, which becomes the perennial rhizome from which the fronds and adventitious roots arise.

In the early stages of embryo development the young sporophyte is completely parasitic upon the gametophyte, just as in the liverworts, obtaining its food and water through the foot. However, as soon as the primary root and leaf are developed, it becomes an independent organism. The gametophyte soon withers, and then the foot ceases to function. Of the four structures mentioned above, only the stem (rhizome) is permanent. It soon develops leaves and adventitious roots, and the primary root and primary leaf die. As in the liverworts and mosses, so also in the ferns, the cells of the gametophyte, including the spores, sperms, and egg cells, have the haploid chromosome number in their nuclei whereas those of the sporophyte have twice that number.

THE CLUB MOSSES

The club mosses, like the scouring rushes or horsetails, constitute a class which was formerly represented by much larger, more numerous, and more highly complex species than exist today. The number of species of living club mosses belong to the two common genera, *Lycopodium* and *Selaginella*.

Remains of certain fossil representatives of this class are abundant in the coal beds. Among the most interesting of these fossil relatives of the modern club mosses are the arborescent genera, *Lepidodendron* and *Sigillaria*. Fossil *Lepidodendron* trunks having a length of over 30 meters have been found. Some of the extinct Lycopodineae had stems in which secondary growth in thickness took place through the activity of a cambium much as in present-day gymnosperms and dicotyledons. The structure of their leaves and stems was much more complicated than in the living species of club mosses.

Selaginella is a type of pteridophyte showing an approach to the seed plants in having well-marked heterospory and a very greatly reduced gametophyte, even though it appears to be in some respects a much more primitive form than the true ferns. In the creeping

species of *Selaginella* the shoot of the sporophyte plant is dorsiventral and the leaves are small and arranged on the axis in four longitudinal rows. The sporophylls are scale-like, generally borne

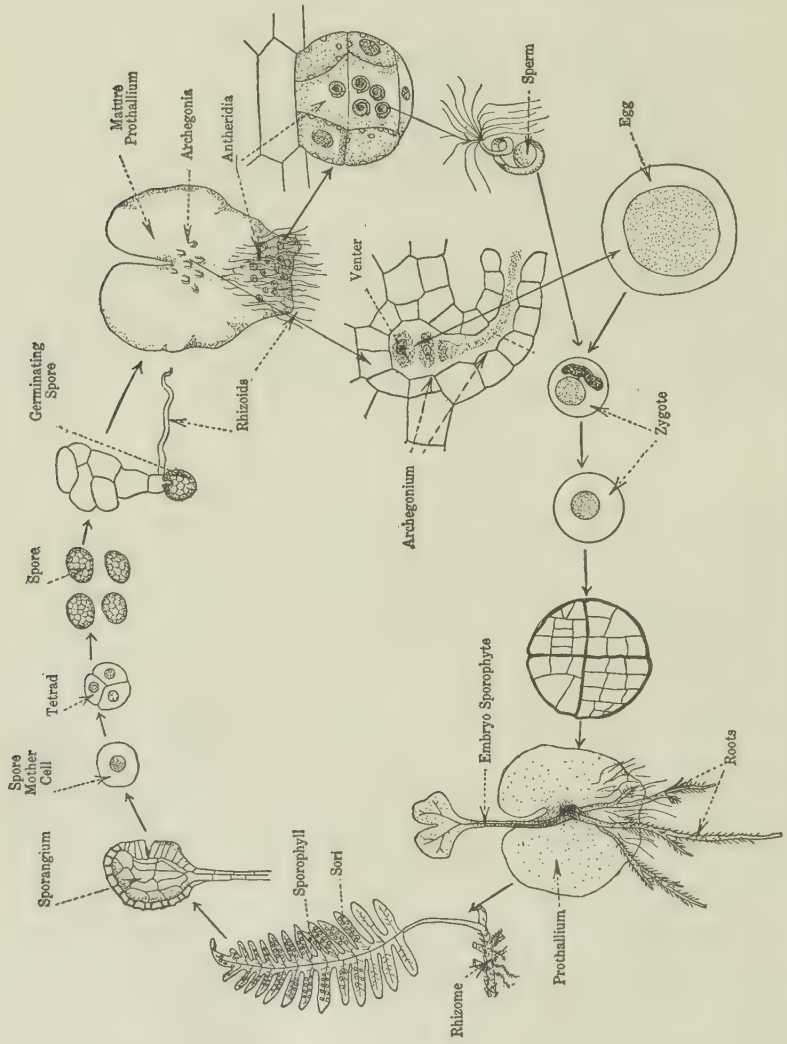


FIG. 241. Diagrams showing stages in the life cycle of a true fern (*Polypodium*).

in four rows so that a rather compact four-angled or club-shaped structure is formed, which feature probably has suggested the common name of "club moss." These cone-like groups of sporophylls are known as **strobili** (singular, **strobilus**).

Selaginella is heterosporous, although *Lycopodium* is homosporous. Heterospory, which is the habit of producing small spores which give rise to male gametophytes and larger spores from which the female gametophytes develop, was characteristic of many of the extinct pteridophytes. Although it is not common among living ferns and fern allies, it is universal among the spermatophytes or seed-bearing plants.

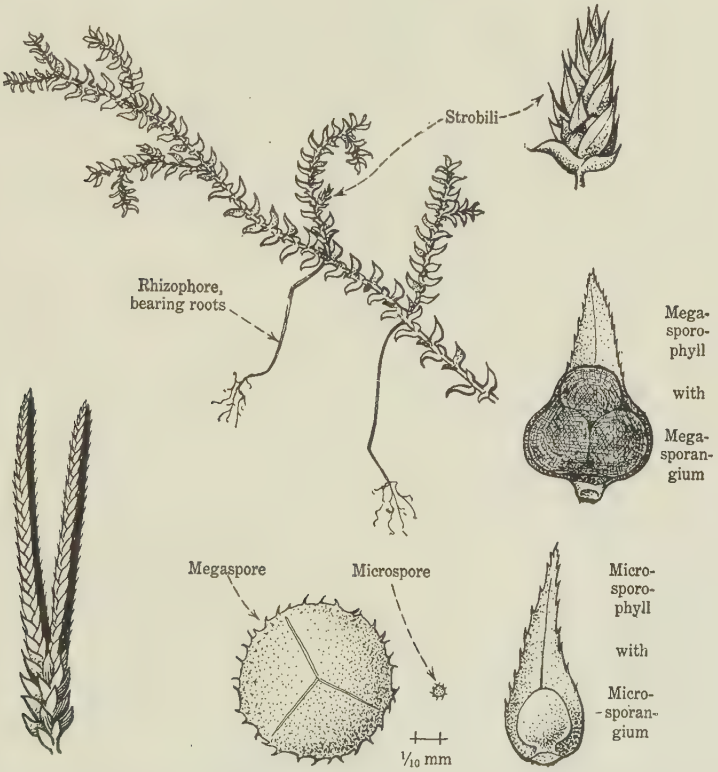


FIG. 242. A species of *Selaginella* showing habit, strobili, microsporophyll, microsporangia, microspore, megasporophyll, megasporangium and megaspore. At the lower left-hand corner are shown two strobili from a different species of *Selaginella*. The 1/10-mm. scale refers only to drawings of the spores.

Corresponding with the difference between the two kinds of spores (**microspores** and **megaspores**) of heterosporous plants are differences in the sporangia (**micro-** and **megasporangia**) and in the sporophylls upon which the sporangia are borne (**micro-** and **megasporophylls**).

The strobili of *Selaginella* are bisporangiate in that they are made up of both microsporophylls and megasporophylls. In *Selaginella* the megasporophylls, each bearing a single megasporangium within which

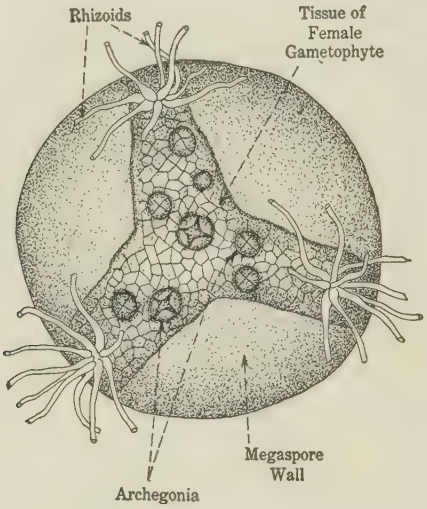


Fig. 243. Female gametophyte of *Selaginella*, partly enclosed by megaspore wall. (Redrawn from Bruchmann.)

four large spores (the megaspores) are produced, are often located near the base of the strobilus. The microsporophylls, which are commonly found nearer the tip of the strobilus, also bear solitary sporangia (microsporangia), but each sporangium contains numerous (generally sixty-four) spores (microspores).

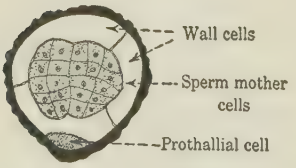


Fig. 244. Male gametophyte of *Selaginella*.

The microspores begin to germinate before they are shed from the microsporangium. This is in marked contrast with conditions in other pteridophytes, but in the Spermatophyta the germination of the microspores is initiated before their release from the sporangium. The male gametophyte of *Selaginella* is formed entirely within the microspore. After the division of the nucleus of the microspore, at the time of its germination, a wall is formed which divides the spores into two cells of very unequal size, the

smaller of which is called the prothallial cell. The spores are usually shed while the contained gametophyte is in this two-celled condition. Subsequently, the larger cell of the two goes through a series of divisions which result in the formation of a central group of cells, and a single layer of wall cells. The protoplast of each cell of the central group develops into a single sperm. The smaller cell of the first two formed (i.e., the prothalial cell) is considered to be homologous with the vegetative cells which make up the greater part of the fern prothallium. All the rest of the gametophyte is believed to represent a single antheridium. The gametophyte is unable to carry on photosynthesis and is entirely dependent upon the sporophyte. This is just the reverse of the condition existing in most liverworts, where the sporophyte is completely dependent upon the gametophyte.

Germination of the megaspores, which generally commences before they are shed from the megasporangium, begins by the division of the single megaspore nucleus into two nuclei, between which no wall is formed. By continued free nuclear division (successive nuclear divisions without wall formation between the resulting nuclei), there develop within the megaspore a large number of nuclei most of which accumulate at one end of the spore. Then walls are formed simultaneously between the nuclei, and thus a mass of tissue (the female gametophyte) arises within the megaspore. By growth of the gametophyte the megaspore wall is finally ruptured at one end and the gametophytic tissue is exposed. Several archegonia develop in this exposed surface.

The archegonia do not differ from those of the true ferns in any important particular. All this development of the female gametophytes takes place, at least in many species, while they are still within the megasporangium, which remains attached to a megasporophyll of the strobilus, the strobilus itself being still attached to the plant.

The male gametophyte is enclosed by the microspore wall at the time when the microspores are shed, and in some species of *Selaginella* the microspores, when shed, sift down between the megasporophylls and come to lie very near the megasporangia. If the plant is wet about this time by rain or heavy dew, the wall separating the sperms breaks down, the contents of the microspore swell, the microspore wall is ruptured, and the biciliate sperms are set free. Previous

to this, the megasporangium wall has cracked open, but not sufficiently to permit the megaspore with the contained female gametophytes to escape. The sperms swim to the archegonia, which are by this time ready for fertilization. The presence of water is essential in order that the sperms may reach the archegonia.

The fertilized egg is the beginning of the (diploid) sporophyte generation, and generally its development into an embryo sporophyte starts at once. The first division of the egg is by a transverse wall

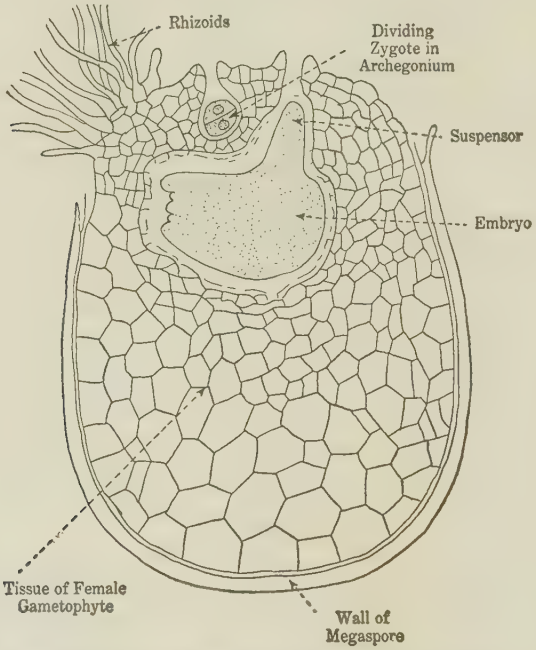


FIG. 245. Longitudinal sections of female gametophyte of *Selaginella*, partly surrounded by the ruptured megaspore wall. One embryo sporophyte is well developed; a second, in its first stage.

and results in the formation of an outer cell known as the **suspensor cell**, and the inner cell, the **embryo cell** from which the embryo proper develops. The suspensor cell greatly elongates, pushing the developing embryo down into the deeper tissue of the female gametophyte, from which nourishment is absorbed. The suspensor is a structure which distinguishes the Lycopodineae from other Pteridophyta, but which occurs in practically all seed-bearing plants. the young embryo, embedded in the tissues of the female gameto-

phyte and still enclosed within the megaspore wall, consists of a foot, a rudimentary root, and a stem growing point with rudimentary leaves.

Although *Selaginella* has many features which by themselves might be interpreted as indicating an approach to the seed plants, it does not seem likely that it or any closely related plant is actually intermediate between the true ferns and the seed-bearing plants.

After the female gametophytes are shed from the strobilus the root soon enters the ground, the stem elongates, leaves are developed, and the young sporophyte becomes independent. The suspensor and foot are temporary structures.

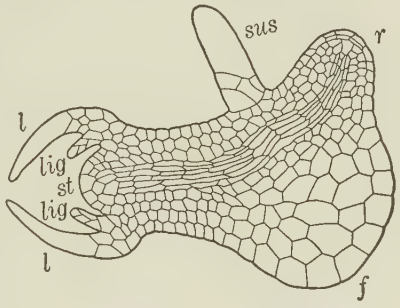


FIG. 246. Embryo sporophyte of *Selaginella*. *sus*, suspensor; *r*, young root; *l*, first leaves; *lig*, ligules; *st*, growing point of stem; and *f*, foot. (Redrawn after Bruchmann.)

Advance of Pteridophyta over the Bryophyta.—We have seen that in the Bryophyta the sporophyte is entirely dependent for its supply of water and mineral salts upon the gametophyte, which alone possesses organs (rhizoids) for absorbing water and solutes from the soil. In many of the Bryophyta the sporophyte is unable to manufacture any of its own food, even though supplied by the gametophyte with water and soil solutes. However, there is a certain approach to independence of the sporophyte in some mosses which have developed chlorophyll-bearing tissue and which could probably live entirely independently if they possessed rhizoids or a root.

It is nevertheless within the Pteridophyta that complete independence of the sporophyte is first attained. Although the sporophyte of the ferns and fern allies is at first attached to the gametophyte by a foot and is for a short time dependent upon it for water and food as well, it soon develops a root which attaches it directly to the soil. By virtue of having a root, the sporophyte is no longer dependent upon the gametophyte for its supply of water and mineral salts. It also possesses leaves, organs which never occur on the sporophyte of the Bryophyta, and a corresponding development of food-manufacturing tissue. This, together with

a well-organized vascular system, efficient epidermis, and a root which can penetrate into the deeper and relatively moister layers of soil, has enabled it to carry on successfully an independent terrestrial existence, which is not possible for the sporophyte of any of the Bryophyta.

The roots of the Pteridophyta and Spermatophyta, although performing the same functions as rhizoids, are structurally far more complex and are capable of indefinite growth.

As to the origin of the Pteridophyta, it is the generally accepted opinion that they and the mosses represent two distinct lines of development from some liverwort ancestor. The Bryales (mosses) have the most complex and highly differentiated sporophyte of any existing plants below the Pteridophyta, but there is little ground for the assumption that the Pteridophyta have arisen from the mosses, even though the mosses are in some respects intermediate between the liverworts and the ferns.

A study of fossil plant remains reveals the fact that the ferns and their allies appeared on the earth earlier than the seed plants. During the carboniferous period (geological age when the great coal beds were deposited), particularly, they were very abundant; in fact, they dominated the vegetation of that time.

Geologists divide the history of the earth into five eras:

1. *Archeozoic*—no life known to have existed.

2. *Proterozoic*—beginnings of life appeared; fossil plants of this era are referred to as Thallophyta.

3. *Paleozoic*—ancient life became well established; the first land plants appeared; during the latter part of the period, particularly in Carboniferous time, Pteridophytes were the dominant element of land vegetation. Representatives of this late Paleozoic flora include large-sized forms resembling our present-day *Equisetum*, tree-size club mosses (*Lepidodendron* and *Sigillaria*), fern-like plants, the so-called seed ferns (Pteridosperms), reproducing by means of seeds rather than by spores, and certain other forms which are now extinct. No flowering plants have as yet been found in rocks of Paleozoic age.

4. *Mesozoic*—known as the age of Cycads because of the abundance of these plants, which are placed in the Gymnospermae. There appeared during this period the immediate ancestors of modern conifers. Flowering plants made their first appearance in the Cretaceous, which is the last period of the Mesozoic era.

5. *Cenozoic*—in which plants and animals of modern types became dominant.

CHAPTER XIV

EMBRYOPHYTA
SPERMATOPHYTA (SEED-BEARING PLANTS)

The fourth division of the plant kingdom, the Spermatophyta, by far exceeds in importance, both economically and as an element in the flora of the earth, all other living plants. To this large group belong the plants which furnish practically all the food, clothing, and shelter of man, and many other useful products. The spermatophytes are the dominant plants of our time and exceed in number of species all the Thallophyta, Bryophyta, and Pteridophyta taken together.

The principal reason for the dominance of the Spermatophyta is the fact that they are more effectively adapted to the land habitat than any other plants. Although the types of the three lower divisions which we have discussed in the preceding chapter, or the smaller groups to which they belong, certainly do not represent an actual evolutionary series which has culminated in the production of the seed-bearing plants, they do probably illustrate roughly some of the principal steps in the evolution of the Spermatophyta. The ancestry of the seed-bearing plants involved members of large groups of plants now extinct.

CHIEF DISTINGUISHING CHARACTERISTICS OF SPERMATOPHYTA

The two characteristics which most sharply differentiate the Spermatophyta from all other plants are (1) the formation of a pollen tube and (2) the production of seeds. These two characteristics are important factors making for the success of the seed plants, first, because the pollen tube has released them from dependence upon water for fertilization and, second, because the seed is a very efficient structure for reproduction and multiplication, being able to

retain its vitality for many years and very resistant to desiccation and to great extremes of temperature. Seeds are also well adapted for wide dissemination, and, because of the well-advanced state of development of the embryo (sporophyte) within the seed and the supply of stored food available to it, the new plant after germination is able to become well established before it must become self-supporting. These facts and the possession of very efficient organs and tissues for absorption, conduction, and conservation of water make it possible for seed plants to thrive in habitats which are much drier than those to which the Bryophyta and Pteridophyta are for the most part restricted.

The seed-bearing plants include species which are adapted to a wide range of conditions. By far the majority are autophytic (that is, are green and make their own food), but a few are heterophytic, as, for example, such saprophytes as Indian pipe (*Monotropa*) and the Sierran snow plant (*Sarcodes*), and such parasitic forms as dodder (*Cuscuta*) and mistletoe (*Viscum* and *Phoradendron*).

In addition to the typical terrestrial forms there are many aquatics, such as the water weed (*Elodea*) and marine eel-grass (*Zostera*), and a large number of epiphytes, mostly tropical or sub-tropical, such as the so-called Florida moss (*Tillandsia*), a member of the pineapple family, and many orchids.

The seed plants have in all probability descended from pteridophyte ancestors, through forms long extinct which were intermediate between certain of the ferns and the most primitive of the Spermatophyta.

The Spermatophyta consist of two well-marked classes, the Gymnospermae (gymnosperms) and the Angiospermae (angiosperms). These two class names are based upon one of the best-defined distinctions between the two groups. The seeds of the Gymnospermae (naked-seeded or cone-bearing plants) are borne upon the surface of the megasporophyll (carpel or cone scale), whereas the seeds of the Angiospermae (covered-seeded or flowering plants) are always formed within a closed structure (the ovary) formed by the union of the margins of one or more megasporophylls (carpels).

GYMNOSPERMAE

The gymnosperms are all woody, perennial forms and with few exceptions are evergreen plants. They are of great economic importance as sources of timber, rosin, and turpentine. The group is a relatively small one, including only about 500 species, whereas there are more than 125,000 species of angiosperms. Among the best-known gymnosperms are those belonging to a group known as the "conifers" which include the pines (*Pinus*), spruces (*Picea*), firs (*Abies*), larches (*Larix*), junipers, frequently but incorrectly called cedars (*Juniperus*), the so-called Douglas fir (*Pseudotsuga*), and the redwood and big tree (*Sequoia*). To the gymnosperms also belong the cycads, some of which resemble tree ferns or palms and are employed as ornamentals, the *Ginkgo* or Japanese maiden-hair tree, and a small group known as the Gnetales, to which belong a number of species of *Ephedra,* a desert shrub, and *Gnetum,* a tropical climber. Gymnosperms are regarded as the most ancient of seed plants. The most primitive living forms are believed to be the cycads.

We shall use the genus *Pinus* as a type of the Gymnospermae since its life history is better known than that of any other representative of the group.

LIFE HISTORY OF THE PINE

With few exceptions, the species of pine have a single main stem or trunk with spreading side branches, which usually appear in whorls. It is an excurrent type of stem, that is, the one main stem maintains its leadership throughout the life of the plant. The foliage leaves are long, slender, and needle-like, and are grouped in clusters of two to five. Pines are "evergreens," that is, at no time in their life are they without leaves. This does not mean that any individual leaf remains on the tree throughout the life of the plant, although it may adhere to its branch for several years; but leaf shedding is going on more or less continuously throughout the year. As in most of the common gymnosperms, the wood contains no vessels, but consists chiefly of tracheids with many bordered pits. The linear form of the leaves, their very thick cuticle, and the depressed stomata show the pines to be xerophytic plants, as in fact are the majority of gymnosperms.

The Cones (Strobili).—The familiar pine tree is the sporophyte (diploid) generation. The spores are borne typically in cones (strobili). Each cone is essentially an axis upon which are spore-bearing leaves, i.e., sporophylls. In pine there are two kinds of cones or strobili: (1) the **carpellate** or megasporangiate cones or strobili; (2) the **staminate** or microsporangiate cones or strobili. They are borne upon the same individual plant.

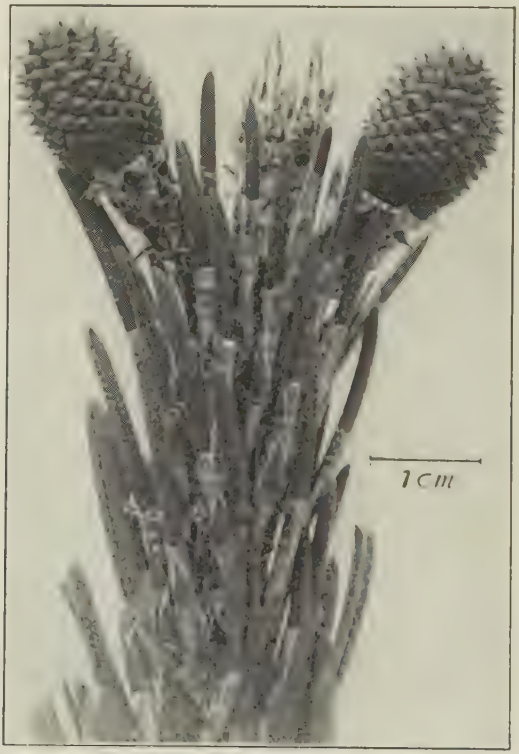


FIG. 247. Tip of a branch of Monterey Pine (*Pinus radiata*), showing two megasporangiate strobili (carpellate cones) a short time after their appearance in the spring and about the time pollination takes place.

Carpellate Cones or Strobili.—The familiar pine cones are the carpellate or megasporangiate or seed-bearing strobili. They remain on the tree for the greater part of two years in all pines, and in some for many years. These cones first make their appearance at the beginning of the growing season when the parts within the buds develop and growth in length of the twigs begins. At

FIG. 248. Sugar pine (*Pinus lambertiana*). 1, mature cone; 2, single carpellate scale with two seeds attached; 3, single mature seed; 4, longitudinal section of seed, showing embryo embedded in endosperm; 5, embryo separated from seed, showing many cotyledons. (After Sargent from *Silva of North America.*)

that time there may be found near the tips of certain branches the newly formed miniature cones (Fig. 247). They seldom exceed a centimeter in length and are generally deep red or flesh color. They consist of a central axis upon which the scale-like megasporophylls are spirally arranged. If one of the megasporophylls is removed from a strobilus and examined with a lens, it will be found to consist of a very short stalk and a scale to which a **bract** is attached on the lower side (Figs. 249 and 251 *A*). On the upper side and near the base of the scale are two rounded or oval swellings. These are the

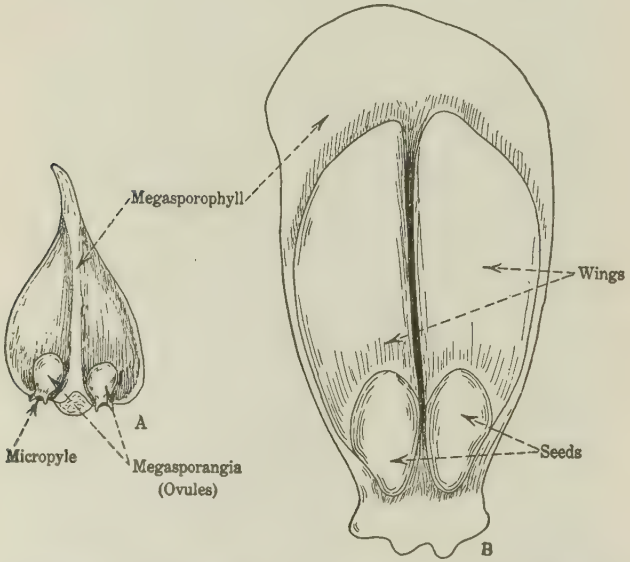


FIG. 249. Megasporophylls of *Pinus*. *A*, about the time of pollination. *B*, after the seeds have matured. Note that the two drawings are made from different species.

megasporangia, or **ovules**, which eventually become the seeds. Sections cut lengthwise through an ovule show that it consists of an oval mass of tissue (the **nucellus**) surrounded by a single **integument**; the micropyle is directed toward the base of the scale (Fig. 255). At the opposite end from the micropyle the tissue of the integument and nucellus is continuous with that of the scale.

Staminate Cones or Strobili.—The staminate or microsporangiate or pollen-bearing strobili are produced in much larger numbers than are the carpellate cones and they are smaller in size.

They are found in clusters near the ends of some of the branches. Like the megasporangiate strobilus, the microsporangiate strobilus consists of a short axis upon which are arranged the microsporophyils in a spiral fashion. They make their appearance at the

FIG. 250. Tip of a branch of *Pinus* bearing microsporangiate strobili (staminate cones). The strobili near the base of the cluster have already shed part of their pollen while in those in the upper part of the cluster the microsporophylls have not separated and no pollen has been liberated.

beginning of the growing season. The microsporophyll consists of a stalk which bears at the end an expanded scale-like portion. The two microsporangia (**pollen sacs**) are attached to the under side of this scale and to the side of the stalk. Generally the

microspores (pollen) are shed within a few weeks after the strobili have made their appearance, whereupon the strobili, having performed their function, wither and soon fall from the tree.

Megasporangium and Megaspores.—Quite early in the development of the carpellate cone, sections of the nucellus of the megasporangium show near its center a single cell which is con-

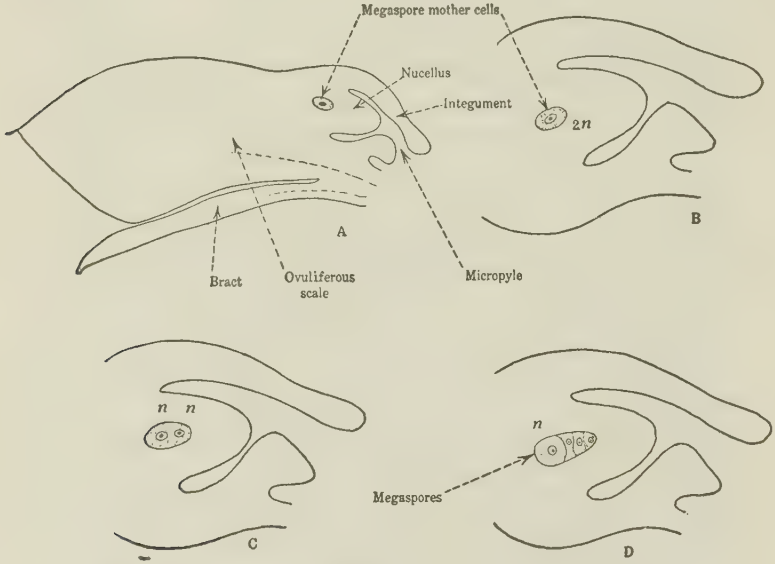


FIG. 251. Diagrams showing the megasporophyll of pine in longitudinal section and four stages in the production of megaspores from the spore mother cell. (*A*, redrawn after Coulter and Chamberlain.)

siderably larger than the surrounding cells and has dense cytoplasm and a large nucleus. (See Figs. 251 *A* and *B*.) This conspicuous cell within the nucellus of *Pinus* soon undergoes two successive divisions, producing four megaspores. The first division marks the beginning of the gametophyte generation, since it is a reduction division reducing the chromosome number from 24 (the diploid number in most species) to 12 (the haploid number). Instead of being arranged in a tetrahedral group as are the spores of all the Bryophyta and Pteridophyta and the microspores of the seed plants, these four spores lie in a row as shown in Figs. 251 *D* and 252. One of the four megaspores, the one farthest from the micropyle, now enlarges at the expense of the other three, which are finally com-

pletely absorbed; thus only one functional megaspore is produced in each megasporangium.

Microsporoangium and Microspores.—The development of the microspores within the microsporangia, in *Pinus*, is not essentially different from the corresponding process in *Selaginella* or from spore production in the true ferns.

The sporangium wall consists of several layers of cells surrounding a group of sporogenous cells which, like all the cells of the pine tree, as we ordinarily know it, have diploid nuclei. By the two successive divisions of each of the cells of this group there

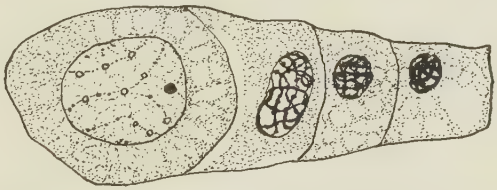


FIG. 252. *Pinus austriaca*. Four megaspores which have arisen by the divisions of the megaspore mother cell within the nucellus. The large basal cell is farthest from the micropyle and is the one which gives rise to the female gametophyte. (Redrawn after Ferguson.)

result the many tetrads of microspores, the nuclei of which have the haploid chromosome number (Figs. 254 *A* and *B*).

Germination of Microspores and Development of Male Gametophyte.—The pollen grains or microspores of *Pinus* germinate (that is, undergo nuclear divisions) as much as a month before they are shed from the microsporangia and months before the germination of the megaspore.

The microspore just before its germination consists of an oval cell with a single large nucleus (Fig. 254 *C*). Each microspore has two balloon-like wings which are air-filled in the ripe spore and each of which may be almost as large as the spore proper. Of the two nuclei formed by the first division of the single nucleus of the spore, one becomes flattened out against the spore wall and is soon cut off from the other daughter nucleus and from most of the cytoplasm of the spore by a thin cell wall (Fig. 254 *D*). This nucleus, the **first vegetative nucleus**, rapidly degenerates. Its sister nucleus has meanwhile undergone a second mitosis. Of the two resulting nuclei, one is the **second vegetative nucleus** and be-

haves like the first vegetative nucleus, and the other, together with the cytoplasm surrounding it, is called the **antheridial cell** (Figs. 254 *E* and *F*). The two vegetative cells apparently perform no function but are merely vestigial cells probably corresponding to the vegetative cells which make up the greater part of the gametophyte of the ferns and to the single vegetative cell of the male gametophyte

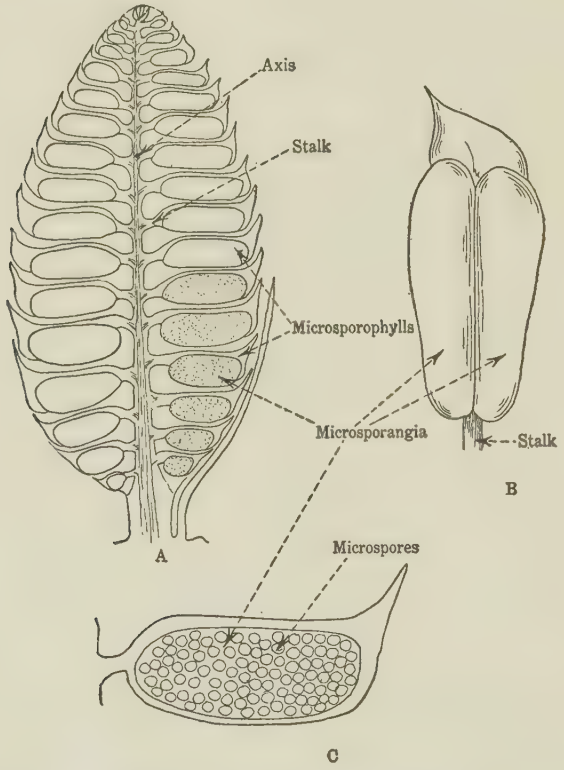


FIG. 253. Microsporangiate strobilus and microsporophylls of *Pinus*. *A*, strobilus in longitudinal section. *B* and *C* two views of a microsporophyll, (the latter in longitudinal section.

which develops within the microspore of *Selaginella*. A short time before the microspores are shed the antheridial cell undergoes division into a smaller cell (the **generative cell**), cut off against the second vegetative cell, and a larger cell (the **tube cell**) (Fig. 254 *F*).

Pollination.—About this time the microsporangia dehisce longitudinally and the pollen grains (microspores) are liberated. The pollen is produced in astonishingly large quantities (that shed

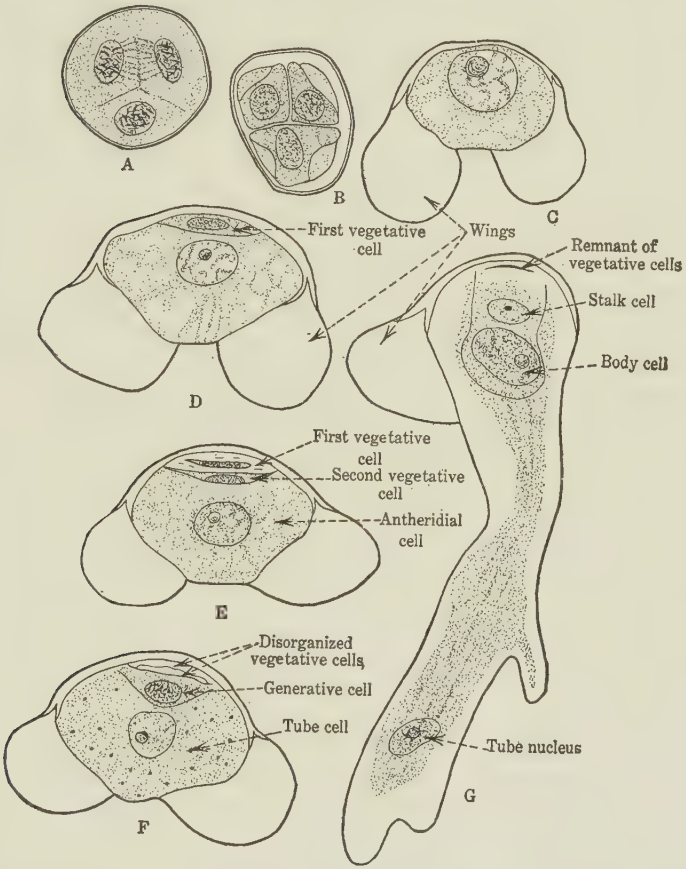


FIG. 254. Successive stages in the development of the microspore and male gametophyte of *Pinus laricio*. *A*, showing the telophase of the second division of the spore mother cell. *B*, showing three of the four spores of a tetrad some time before maturity. *C*, a mature microspore. *D* to *F*, successive stages in the development of the male gametophyte up to the time the spores are shed. *G*, about a year after pollination and some time before fertilization. (Redrawn from Coulter and Chamberlain.)

by a single Scotch pine may be as much as a quart), and the pollen grains may remain floating in the air for a long time. There are records of pine pollen having been borne for several hundreds of miles by the wind. Pine pollen is yellow and resembles in color

and texture the finely powdered form of sulphur called "flowers of sulphur."

As in all wind-pollinated plants, by far the greater part of the pollen is wasted. Some does, however, reach the carpellate cones, the megasporophylls or scales of which at this time are slightly separated, so that some of the pollen grains sift down between them and come to lie in close proximity to the micropyles of the ovules. Just at this time the nucellus in each ovule exudes a quantity of a sticky fluid, which protrudes through the micropyle and comes in contact with some of the microspores. As the drop dries, the pollen grain or grains are drawn down through the micropyle and come in contact with the nucellus itself. Pollination is different from that of the angiosperms in that in *Pinus* and many related gymnosperms the pollen grain, instead of being brought into contact merely with the stigma (tip of the carpel or carpels), is brought into direct contact with the nucellus of the ovule.

Subsequent Changes up to Fertilization.—At the time of pollination the pollen grain contains a male gametophyte consisting of (1) two flattened and much-disorganized vegetative cells, (2) the generative cell, and (3) the tube cell (Fig. 254 *F*). The ovule at this time is in the condition already described, the nucellus or megasporangium proper being surrounded by a single integument and enclosing a single functional megaspore which is larger than the surrounding cells but lacks any thick spore wall such as is found in *Selaginella*.

Very soon after pollination the scales of the carpellate cone become closely pressed against each other as a result of their growth, and they are sealed together by an exudation of pitch. Later the cone is inverted by the curvature of its stalk. During the subsequent eleven months the male gametophyte does not develop to any considerable extent. A short pollen tube is formed by each pollen grain. This tube, which may branch somewhat, penetrates the tissue of the nucellus and grows downward very slowly until growth is interrupted by cold weather.

Development of Female and Male Gametophytes.—During the year following pollination there is developed from the megaspore a considerable mass of tissue which is the female gametophyte, and which is often spoken of as the endosperm.

In the development of this female gametophyte, or endosperm, the megaspore first enlarges considerably at the expense of the nucellar tissue which surrounds it. It then germinates, i.e., undergoes division of its nucleus into two nuclei. These two nuclei are not separated by a wall, however, and they undergo repeated division without wall formation. After this free nuclear division has continued for some time, walls are formed between the nuclei, and there results a solid mass of gametophyte tissue which has displaced a considerable amount of the tissue of the nucellus.

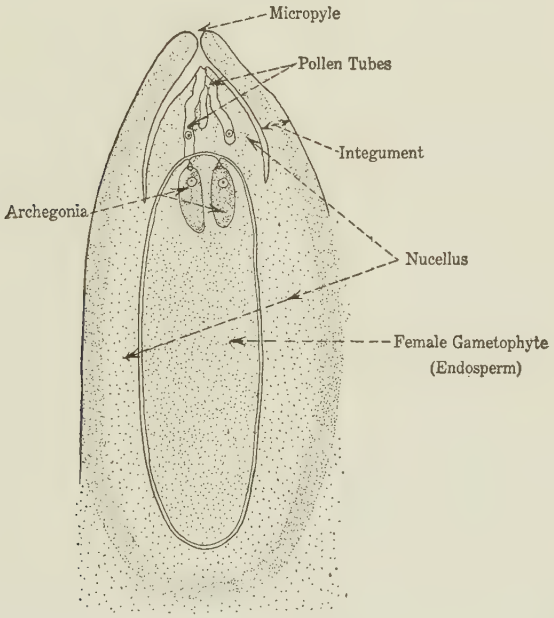


FIG. 255. Ovule of pine at about the time of fertilization. (Redrawn after Coulter and Chamberlain.)

Late in the spring of the following year (nearly a year after pollination) there are formed at the end of the female gametophyte nearest the micropyle a number of archegonia, generally two or three (in some species of gymnosperms as many as sixty), which are quite different in appearance from those of the Pteridophyta. Each archegonium has its origin in a single superficial cell of the gametophyte, and no part of it projects above the surface of the gametophyte (Fig. 255). The cavity in which the

egg lies is surrounded by a layer of cells, the **jacket cells,** which have dense cytoplasm and large nuclei. The jacket cells supply food to the egg cell and later to the embryo. The archegonium is not fully developed and ready for fertilization until about a year after pollination.

During the second spring the pollen tube, which had ceased development during the cold winter months, begins growing slowly

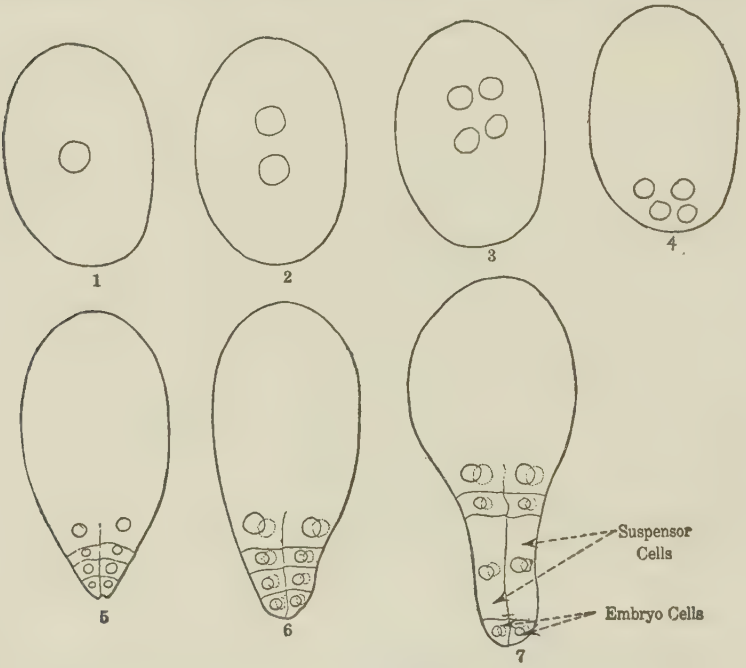


FIG. 256. Diagrams showing stages in the development of the pro-embryo of *Pinus* from the zygote; 1, shows the zygote before the first division of the fusion nucleus; 2 to 7, see explanation in the text.

downward and penetrating the nucellar tissue which caps the apical portion of the female gametophyte. The tube nucleus has by this time passed from the body of the spore into the tube. Meanwhile the generative cell has divided into a **stalk cell** and a **body cell** (Fig. 254 *G*), which also soon pass into the tube. In the tube the nucleus of the body cell divides into two nuclei which are the sperm nuclei and correspond to the sperms of *Selaginella* and other Pteridophyta and of the Bryophyta. Thus the fully developed male

gametophyte consists of two disorganized vegetative cells in the body of the spore and four cells which lie in the tube and are not separated from each other by cell walls. The cells in the tube are (1) the tube cell, (2) the stalk cell, and (3) two male gametes or sperm cells. The nuclei of the sperm cells are large and stain more densely than do the other nuclei in the tube, and their cytoplasm is quite clearly differentiated.

Fertilization.—When the tip of the pollen tube reaches the surface of the female gametophyte, it discharges the four cells which it contains into the cytoplasm of the egg.

The nucleus of one (the functioning) male cell now moves toward the large egg nucleus which lies deep in the cytoplasm of the egg cell, and fusion of the two gamete nuclei takes place. The non-functioning male nucleus and the tube and stalk nuclei soon undergo disorganization, their material becoming part of the food store of the zygote.

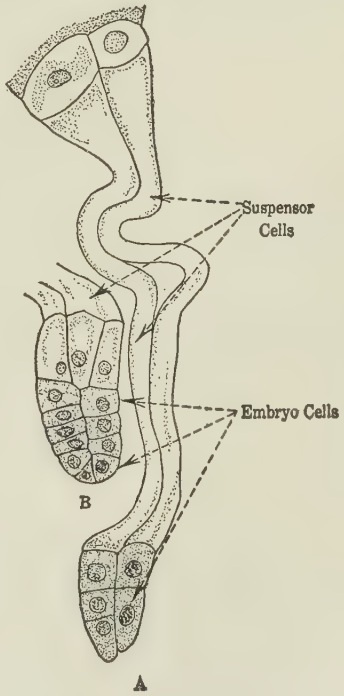


FIG. 257. Further development of the pro-embryo of pine, showing early stages (*A* and *B*) in the development of the embryos. (Redrawn after Coulter and Chamberlain.)

Formation of the Embryo.—Immediately upon the fusion of the functioning male nucleus and the egg nucleus, the zygote nucleus begins to divide. By successive divisions sixteen cells (four tiers of four) are produced, of which the uppermost four are not cut off from the cytoplasm of the egg (Fig. 256). This group of sixteen cells is called the **pro-embryo.** Of the four tiers of cells of the pro-embryo, those in the next to the lowest tier elongate to ten or twelve times their original length (Figs. 257 and 258 *A*). They are called suspensor cells, and their elongation causes the four cells of the lowermost tier to be pushed deep down into the endosperm (female gametophyte tissue) below the archegonium. The eight cells of the two upper tiers remain

within the cavity of the original egg cell and serve to absorb food for the nourishment of the four embryo cells, each of which develops into an embryo. Since there may be three archegonia within a single pine ovule, as many as twelve young embryos may thus be formed. Before their development has progressed far, one generally surpasses the others and finally develops at their expense into the one functioning embryo of the seed.

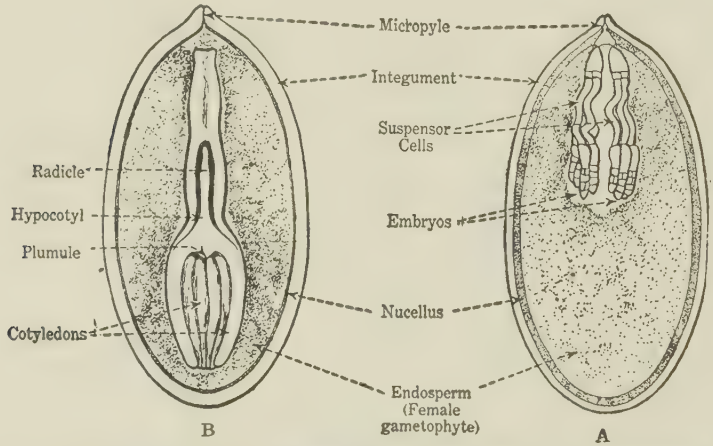


FIG. 258. Two stages in the development of pine seed, shown in longitudinal section. *A*, more highly magnified than *B*, and showing an earlier stage of development. Note the numerous embryos in *A* and the single surviving embryo in *B*, also the greater relative reduction of the nucellus in the older seed. (Redrawn from Curtis.)

The Seed.—Even after fertilization the endosperm continues to grow, encroaching upon the tissue of the nucellus and absorbing it. Accordingly, in the ripe seed nothing remains of the nucellus but a brown, papery layer capping the endosperm at the micropylar end of the seed. Buried in the endosperm of the mature seed is the embryo, which consists of the **radicle**, the **hypocotyl**, three to eight **cotyledons**, and the **plumule** (Fig. 258). The shell, or seed coat, of the pine seed is formed by changes in the tissue of the integument. In many pines a layer of tissue from the upper surface of the cone scale splits off to form a wing, which remains attached to the base of the seed when it is shed. This imparts a spinning motion to the seed as it falls, and slows its rate of descent so that in a moderate breeze the seeds may be carried some distance from

the tree on which they are produced. The germination of pine seeds does not differ in any very significant particular from that of the angiosperm seeds discussed in an earlier chapter. After fertilization and while the ovule is developing into a seed, the whole carpellate cone grows to many times its previous size, and the tissues of the cone scales become woody and hard and lose most of their water. In most species the scales separate after the seeds have become mature, and allow the seeds to escape.

FLOWERING PLANTS (ANGIOSPERMAE)

The second class of the Spermatophyta, the Angiospermae, far exceed in number of species and in importance to man any other class in the plant kingdom. In fact, in the number of known species the angiosperms exceed all the other plant groups taken together. With the exception of certain gymnosperms which furnish timber, turpentine, and rosin, the group contains the vast majority of plants that are utilized by man as a source of food, clothing, or materials for use in industry and in the arts. Although angiosperms include some very simple forms which have evolved by reduction from more highly differentiated forms, without question they represent the highest point in the evolution of plants.

The angiosperms as a class are better adapted to the land habitat than any other class of plants. Accordingly they are not only the most important and conspicuous element in the flora of the earth but are represented in practically every part of the world where plants can live at all.

The characteristic organ of the angiosperms is the **flower**. The typical flower is a very specialized shoot, consisting of an axis bearing a number of sporophylls (spore-bearing leaves)—microsporophylls (stamens) and megasporophylls (carpels). Angiosperm seeds are borne within a closed structure (ovary), presumably resulting from the fusion of the edges of one or more megasporophylls. It will be recalled that the seeds of the gymnosperms almost always are borne naked on the surface of megasporophylls, which do not form ovaries.

The angiospermae consist of two sub-classes, the **Monocotyledonae** and the **Dicotyledonae**. The second of these contains many

more species than the first. Of the several characteristics distinguishing the two classes from each other one of the most striking is the number of cotyledons in the embryo, there being one in the monocotyledons, and two in the dicotyledons. The grasses, including cereals (wheat, oats, barley, rye, rice, corn and sorghums), the lilies, the

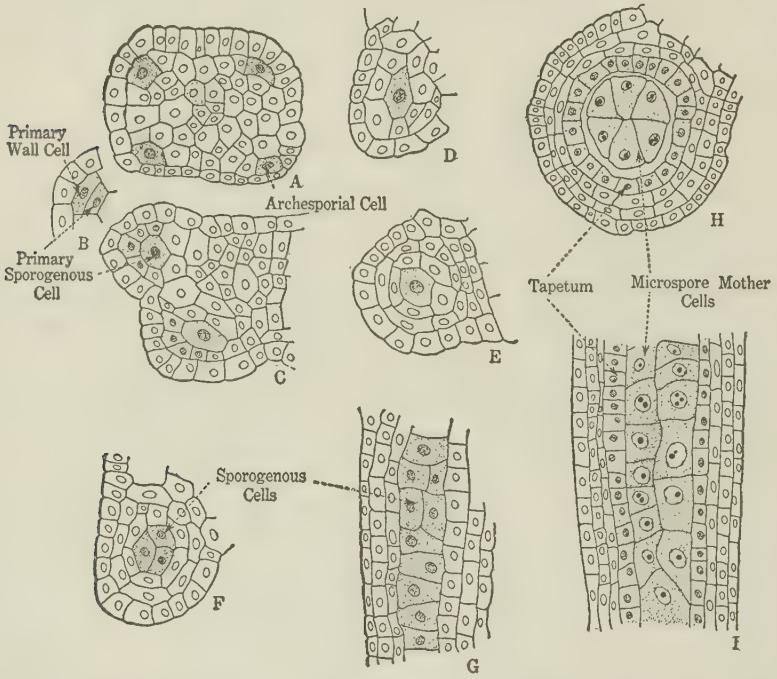


FIG. 259. Stages in the development of the anther of wheat. *A*, cross section of young anther. *B*, first division of archesporial cell. *C*, *D*, *E* and *F*, cross sections of anthers showing subsequent division. *G*, longitudinal section of *F*. *H* and *I*, cross and longitudinal sections of a locule of a young anther, showing mature microspore mother cells. (Redrawn from Percival.)

palms, and orchids, are among the principal families of the monocotyledons. Most other common angiosperms are dicotyledons.

Life History of Wheat (Triticum).—Among the several thousand genera of angiosperms, there is, for the most part, marked uniformity in the essential stages of their life history. As the angiosperm representative, we have chosen *Triticum aestivum* (common wheat), not only because its life history has been rather completely worked out, but also because it is one of the most important

and familiar plants in the world. Inasmuch as the origin and development of the seed are essentially the same in *Zea* (Indian corn), illustrations of some stages have been taken from the latter plant.

As in the Pteridophyta and in Gymnospermae, the sporophyte of wheat, and of the other angiosperms, is the conspicuous generation in the life history, i.e., the sporophyte is "the wheat plant." It consists of root and shoot, the latter made up of the stems and leaves. In addition to foliage leaves there are floral leaves.

The principal features of a grass flower are shown on page 164 (Fig. 114). The flower proper consists of a single pistil with three carpels (two abortive), three stamens, and two small scale-like structures (lodicules) which lie at the base of the ovary. The lodicules are regarded as modified perianth sigments. The ovary contains a single ovule and has two feathery, much-branched stigmas. The stamens and carpels of all angiosperms correspond to the microsporophylls and megasporophylls of *Selaginella* and *Pinus*. In this chapter we shall use the terms microsporophylls and megasporophylls, rather than the terms stamens and carpels, which originated long before the true relation of these structures to the spore-bearing leaves of the gymnosperms and pteridophytes was understood.

Microsporophyll (Stamen) and Microsporangium (Pollen Sac).—The anther consists at first of a small mass of meristematic cells (Fig. 259). There are early differentiated in this mass four separate groups of cells, which by further development will become the microsporangia. Each of these groups includes a longitudinal row of cells (the **archesporial cells**) which are just beneath the epidermis and which are conspicuous by reason of the dense appearance of the cytoplasm and their large nuclei. Each cell of this row divides, by a wall parallel to the surface of the anther, to form two cells. Thus two rows are produced. By further division of the cells of the outer row (**primary wall cells**) several layers of cells are formed, and these, together with the epidermis, make up the wall of the microsporangium. By repeated division of the cells (**primary sporogenous cells**) of the inner of the two original rows, cells (**microspore mother cells**) are formed, each of which gives rise to four microspores (pollen grains). The microspores are pro-

duced in groups of four. One of the last two divisions giving rise to these spores is a reduction division and reduces the chromosome number of the nuclei to the haploid number, and thus the male gametophyte stage begins.

Megasporophyll (Carpel) and Megasporangium (Nucellus).—The megasporangium has its origin in a small mass of undiffer-

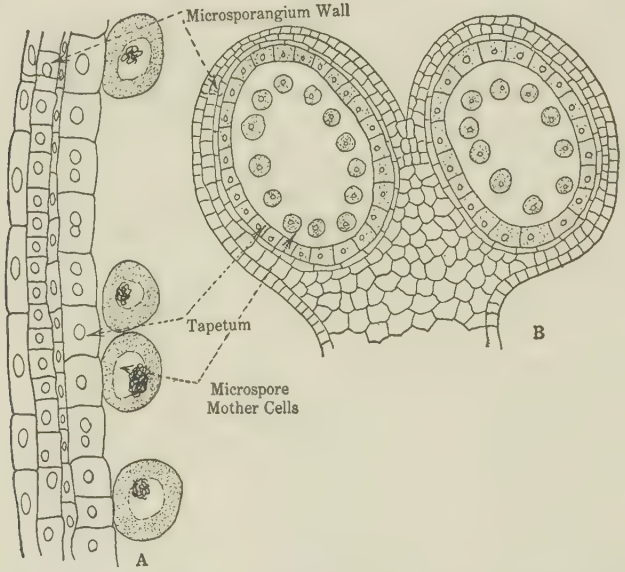


FIG. 260. *A*, longitudinal section of a portion of the wall of the anther of wheat. *B*, transverse section of an anther lobe of wheat. (Redrawn from Percival.)

entiated cells which protrude from the placenta. From the base of this projection arise two rings of tissue which grow up about the developing megasporangium. These two layers of tissue (the integuments) finally entirely envelop the megasporangium proper, except for a small opening (micropyle) at the free end of the ovule.

While the megasporangium is still very small, one of the cells just below the epidermis of the nucellus becomes differentiated from the surrounding cells in size and in appearance of its contents (Fig. 261 *A*).

The nucleus of this cell now undergoes two successive divisions one of which is a reduction division and reduces the chromosome

number of the nuclei from $2n$ (the diploid number) to n (the haploid number) and thus initiates the female gametophyte stage of the life cycle. These divisions give rise to four potential megaspores (Figs. 261 *B* and *C*). These spores are not arranged in the characteristic tetrahedral groups, as are the spores of all Bryophyta and Pteridophyta and the microspores of seed plants, but in a

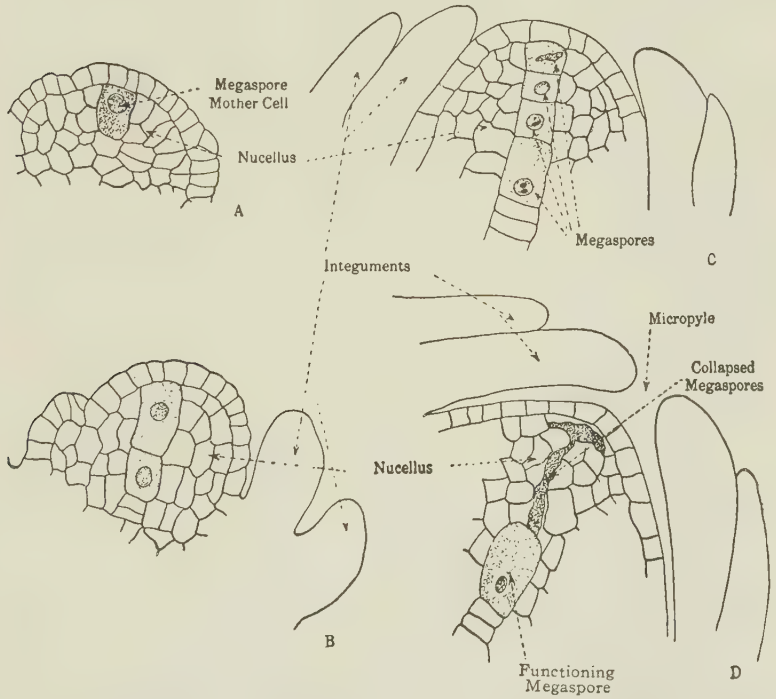


FIG. 261. Median lengthwise section of young ovules of wheat, showing development of the megaspores and the degeneration of all but one of these. (Redrawn from Percival.)

straight row. Definite walls are formed around each megaspore. Soon the basal megaspore (the one farthest from the micropyle) begins to enlarge at the expense of the other three, and finally these three are completely absorbed, leaving a single large functioning megaspore, as in *Pinus* (Figs. 261 *D* and 263 *A*).

The Male Gametophyte.—Germination of the microspore (pollen grain) begins while it is still within the microsporangium (pollen

sac of the anther). For convenience we shall consider the germination of the microspore and the development of the male gametophyte as taking place in the following stages:

1. Division of the protoplast of the microspore into a tube cell and a generative cell. The cytoplasm of these two cells is clearly differentiated, but they are not separated by a wall. (See Figs. 126 and 262).

2. A little later, but, in wheat, before the shedding of the microspores, division of the generative cell to produce two male gametes. (In many angiosperms the second division does not take place until after the pollen tube is formed.)

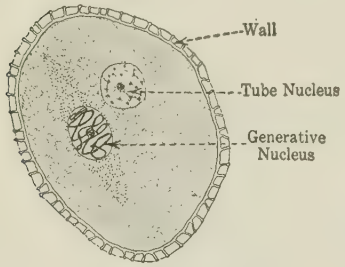


FIG. 262. Pollen grain of Lilium at time of shedding. Early stage of a male gametophyte enclosed within the microspore wall.

3. After pollination, the formation of the pollen tube.

4. Migration of the two male gametes, the tube nucleus, and cytoplasm from the pollen grain into the pollen tube.

The mature male gametophyte, consisting of three nuclei and some associated cytoplasm, is even more reduced than in *Pinus*, in which, in addition to the two sperm nuclei, there are two vegetative cells, a tube cell, and a stalk cell. (Compare Figs. 254 *F* and *G*.)

The Female Gametophyte (Embryo Sac).—The protoplast of the single functioning megaspore now undergoes free nuclear division, as in *Pinus* and *Selaginella*. There results a female gametophyte consisting of eleven to fifteen nuclei lying free in a mass of vacuolated cytoplasm.

This process of development of the female gametophyte may be conveniently divided into the following stages:

1. The first division of the megaspore nucleus results in two nuclei which promptly separate; one of these moves to the micropylar end of the sac, and the other goes to the opposite (antipodal) end of the sac.

2. Each of these two nuclei divides, so that there are two nuclei at the micropylar end, and two at the antipodal end.

3. After this second division, each of the four nuclei divides, resulting in eight nuclei, four at the micropylar end and four at the antipodal end.

4. Now, a single nucleus from each group of four moves

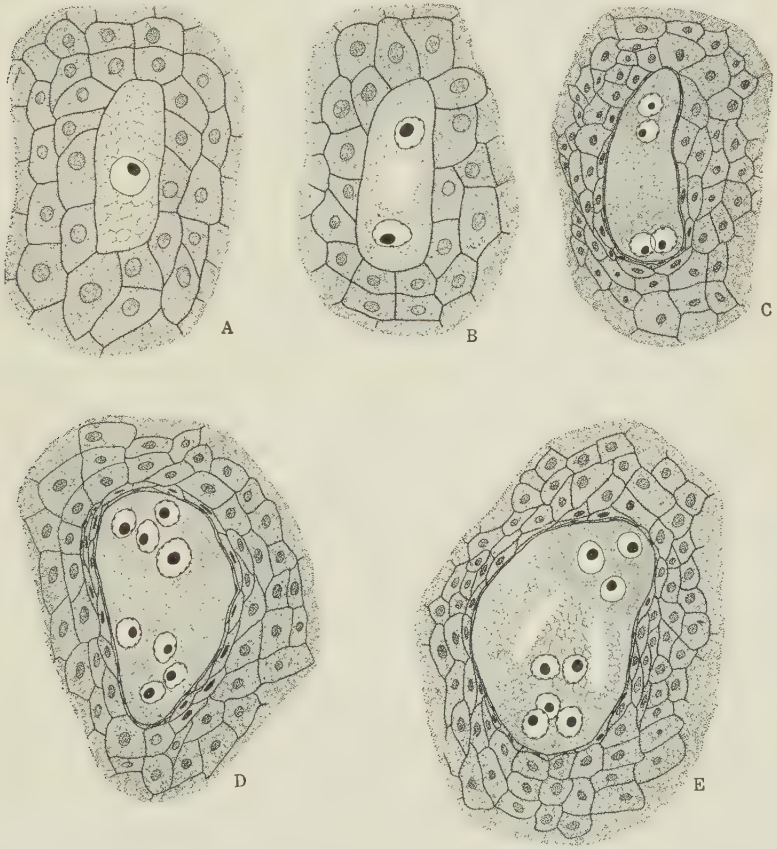


FIG. 263. Stages in the development of the female gametophyte (embryo sac) of corn. Longitudinal sections. *A*, 1-celled embryo sac (megaspore). *B*, 2-celled embryo sac. *C*, 4-celled embryo sac. *D*, 8-celled embryo sac at time the polar nuclei have started to migrate. *E*, 8-celled embryo sac after the polar nuclei have migrated. The megaspore mother cell and embryo sacs are embedded in nucellar tissue. (Redrawn from Miller, in *Journal of Agricultural Research*.)

toward the center of the embryo sac. The two nuclei (polar nuclei) lie in contact with one another without fusing until the time of fertilization.

5. The three nuclei at the end opposite the micropyle divide, forming a group of six to eight antipodal nuclei. Although not separated from one another by cell walls, each of these nuclei has about it a quantity of cytoplasm set off from that of neighboring nuclei, so that we may speak of each nucleus and its associated cytoplasm as a cell (antipodal cell). In many angiosperms there are only three antipodal cells.

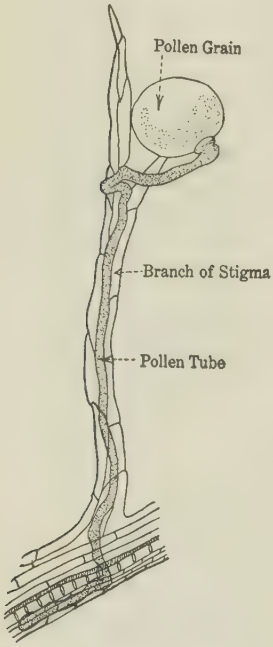


FIG. 264. Single branch of the stigma (silk) of corn (*Zea mays*), showing path of the pollen tube. (Redrawn from Miller, in *Journal of Agricultural Research.*)

6. Of the three nuclei remaining at the micropylar end, one is the egg nucleus, and the other two are the synergid nuclei. Each of these nuclei has associated with it a quantity of cytoplasm, although no walls separate these nuclei from each other. Thus at the time of fertilization the female gametophyte of wheat (see Figs. 263 and 265 and compare Fig. 110) consists of:

(*a*) Two synergids or "helper cells" at the micropylar end of the embryo sac.

(*b*) A single egg cell near the synergids.

(*c*) Two polar nuclei, usually near the center of the embryo sac.

(*d*) Six to eight antipodal cells, at that end of the embryo sac which is opposite the synergids.

Pollination and Development of the Pollen Tube.—The pollen of wheat is carried to the plume-like stigma by the wind. Within an hour and a half to two hours after pollination the pollen tube begins to develop (see Fig. 264). It penetrates the tissue of the stigma and, entering the hollow style, grows downward into the ovary, where it finds its way to the micropyle. After passing through this opening, it penetrates the tissue of the nucellus and enters the embryo sac. (See Fig. 265.)

There is considerable variation in different angiosperms as to the length of the interval between pollination and fertilization. In wheat the union of the male gamete with the egg nucleus has

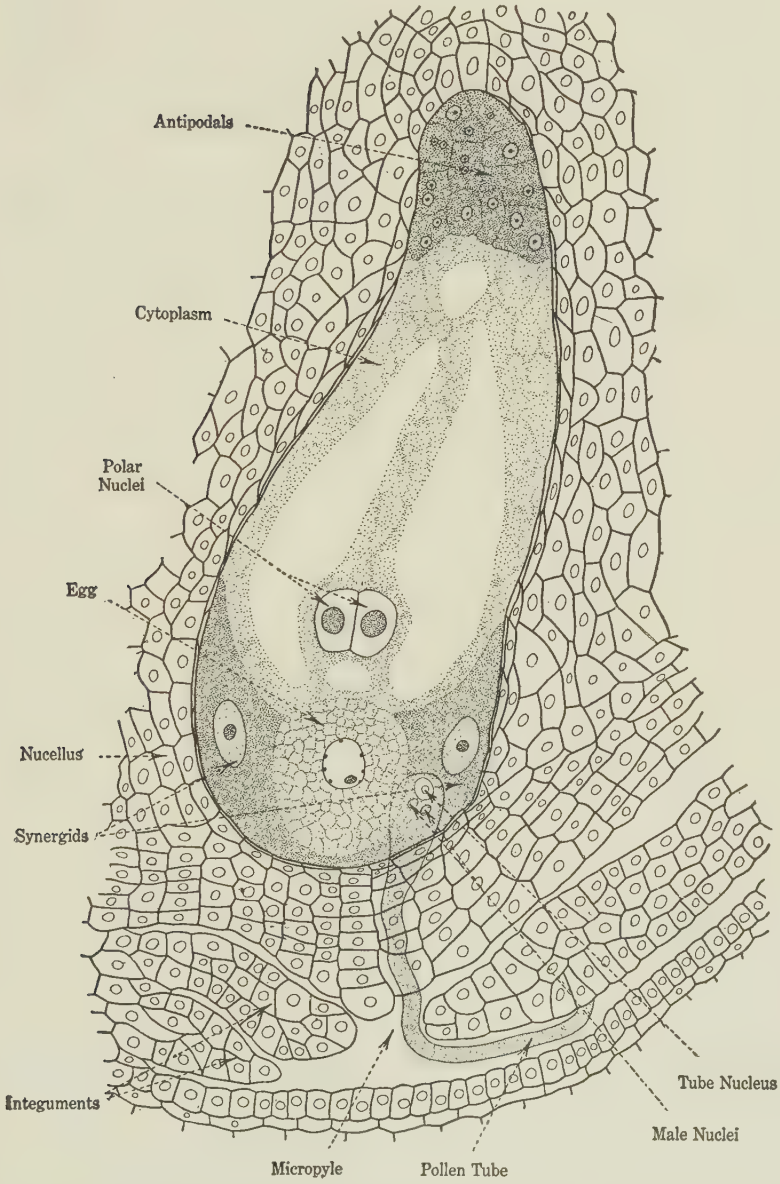


FIG. 265. Longitudinal section of a mature embryo sac of corn (essentially similar to that of *Triticum*) (*Zea mays*) just prior to fertilization. Redrawn from Miller, in *Journal of Agricultural Research*.)

been observed between thirty and forty hours after pollination. In most angiosperms the time interval between pollination and fertilization is from a few hours to several days, but there are species (elms, oaks, walnuts, orange, etc.) in which fertilization does not take place until almost a year after pollination.

Fertilization.—Soon after penetrating the embryo sac the tip of the tube is ruptured and its contents discharged. One of the sperm nuclei fuses with the egg nucleus to form the zygote nucleus, and the second sperm nucleus unites with the polar nuclei to form the endosperm nucleus. (See Figs. 266 and 267.)

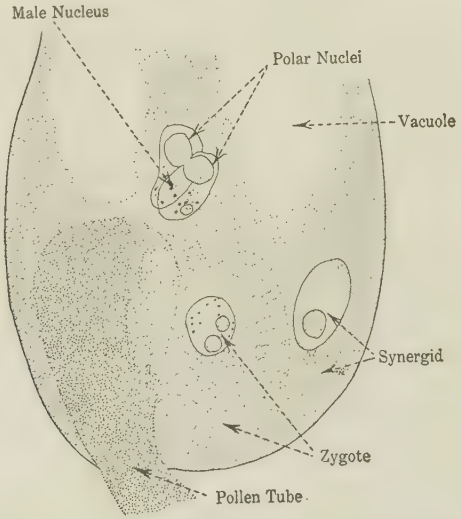


FIG. 266. Longitudinal section of the lower portion of the embryo sac of corn at the time of fertilization. One male nucleus is shown fusing with the two polar nuclei, and the other male nucleus is shown fusing with the egg nucleus. (Redrawn from Miller, in *Journal of Agricultural Research.*)

At the union of a sperm nucleus with the egg nucleus, the resulting zygote marks the beginning of the new sporophyte (diploid) generation, that is, the new wheat plant. The endosperm nucleus, resulting from the union of the second sperm nucleus with the two polar nuclei, and therefore having $3n$ chromosomes, initiates the formation of the endosperm.

By the union of the sperm with the egg, the zygote is furnished with one set of chromosomes from the male parent and another

set from the female parent. Thus the zygote has the diploid chromosome number characteristic also of all the nuclei of the sporophyte which develops from the zygote. These two sets are associated in all the cells of the sporophyte. That is, in the first division of the zygote nucleus and in all subsequent divisions of the sporophyte cells, chromosomes of paternal origin (contributed by the sperm nucleus) and those of maternal origin (contributed by the egg nucleus) split longitudinally, and each daughter nucleus receives an equal part of each maternal and paternal chromosome. There is reason to believe that the chromosomes contributed by the male and female gametes respectively maintain their individuality in the nuclei of all sporophyte cells, although the total quantity of chromatin increases with each nuclear division.

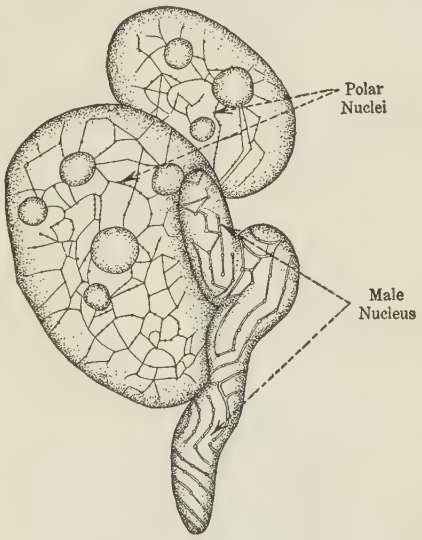


FIG. 267. Fusion of male nucleus with two polar nuclei, in *Lilium aurantum*, to form the primary endosperm nucleus, ×1260. (Redrawn from Blackman and Welsford.)

The synergids degenerate at about the time of fertilization. During the growth of the embryo and endosperm, the antipodal cells also slowly undergo disorganization.

Development of Embryo Sporophyte (Wheat Plant).—The fertilized egg (zygote) becomes by repeated division a multicellular embryo sporophyte. In wheat, the zygote undergoes division into two cells (this stage is not shown in the figures) a few hours after fertilization. The larger of these two cells is the suspensor, and from the smaller cell the embryo develops. A depression appears at one side of the embryo, marking the position of the growing point of the stem. The scutellum (single cotyledon) arises from the tissue above this depression. The origin and development of the other organs of the embryo are shown in Fig. 269.

It will be observed that in wheat the growing point has a

lateral origin and the cotyledon is terminal in origin. This type of embryo development contrasts with that found in most dicotyledons, as illustrated in *Capsella* (see Fig. 127), in which the growing point is terminal in origin and the cotyledons are lateral in origin.

Development of the Endosperm (Reserve Food Supply).— In *Pinus* and in most other gymnosperms the nutritive tissue of the seed, the endosperm, is the female gametophyte, a mass of tissue

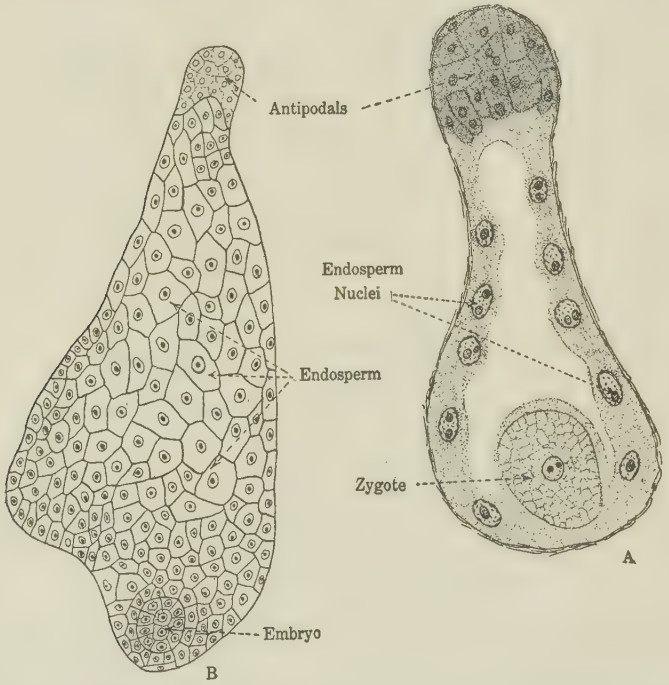


FIG. 268. *A*, longitudinal section of the embryo sac of corn 12 hours after fertilization. *B*, 36 hours after fertilization. (After Miller, in *Journal of Agricultural Research.*)

with haploid nuclei, developed by repeated divisions of the megaspore. Even at the time of fertilization, this gametophyte tissue makes up, in *Pinus,* a considerable part of the ovule, and after fertilization it continues to grow until it finally displaces all the tissue of the nucellus. In wheat and all other angiosperms the endosperm has an entirely different origin. It is initiated, not by the germination of the megaspore, as in *Pinus,* but by the division of the endosperm nucleus of the fertilized embryo sac.

Although the first division of the zygote nucleus is followed by wall formation and all the cells of the embryo are enclosed in cell walls, the endosperm develops at first by free nuclear division, that is, repeated division of nuclei without cell wall formation. This process has already been met with in the development of the female gametophytes of *Selaginella* and *Pinus*. In wheat, walls are later formed between the free nuclei, and the endosperm tissue results, the cells of which contain large quantities of stored food.

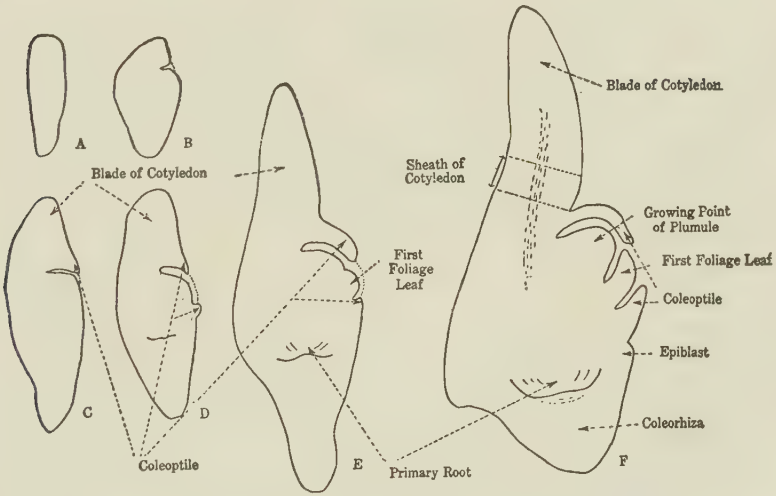


FIG. 269. Longitudinal sections of the embryo of wheat in various stages of development. (Redrawn from Percival.)

It will be recalled that in many plants, such as peas, beans, alfalfa, squash, and sunflower, the endosperm is completely absent in the mature seed owing to its absorption by the developing embryo previous to the maturing of the seed. In wheat, as in all other grasses, and in the castor-oil plant, and many other angiosperms, the endosperm constitutes a large part of the mature seed, performing its function of supplying food to the embryo after germination begins, not before the seed matures.

The Seed.—In the enlargement of the embryo and endosperm, the tissue of the nucellus is encroached upon and either partially or totally absorbed. In the mature wheat seed the nucellus constitutes a thin layer of cells covering the outer surface of the endosperm. In the young wheat seed there are also two integuments, each

consisting of two layers of cells. In the maturing of the seed the outer integument is entirely absorbed, so that the mature seed coat has but two rows of cells belonging to the inner integument. It will be recalled that the so-called "seed" or grain of wheat is in reality a one-seeded fruit, in which the ovary wall has become firmly attached to the ovule.

Thus, as a result of nuclear fusions in the embryo sac, which is embedded in the megasporangium (nucellus of the ovule), there

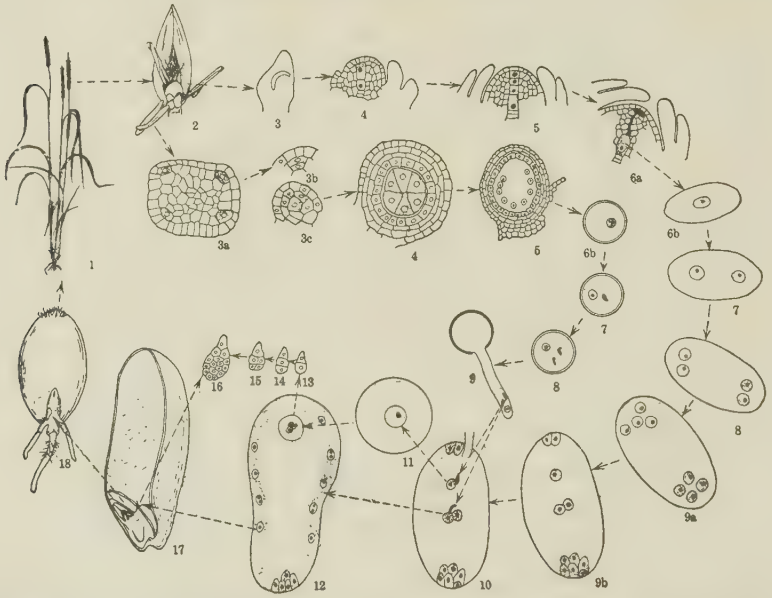


FIG. 270. Diagrams showing stages in the life cycle of wheat. 1, mature sporophyte; 2, single flower; (outer circle) 3, 4, 5 and 6*a* and 6*b*, stages in the development of the megaspore; (inner circle), 3*a*, 3*b*, 3*c*, 4, 5, and 6*b*, stages in the development of the microspore; (outer circle), 7, 8, 9*a* and 9*b*, stages in the development of the female gametophyte; (inner circle), 7, 8 and 9, development of the male gametophyte and germination of pollen grain; 10, process of double fertilization; 11, zygote; 12, developing zygote and endosperm within the embryo sac; 13, 14, 15, 16, early stages in the development of the embryo sporophyte; 17, mature grain in longitudinal section showing mature embryo and endosperm (dotted); 18, germinating embryo.

follows a series of changes, involving all the tissues of the ovule, which result in a structure termed the seed. The mature wheat seed possesses tissue belonging to (1) the **parent sporophyte**, (2) the **embryo sporophyte**, and (3) the **endosperm**, which cannot properly be designated either as sporophytic or gametophytic inasmuch as its cells theoretically, and actually as has been shown in

some cases, have nuclei with $3n$ chromosomes. The seed coats and the nucellus belong to the parent sporophyte.

Important Points of Contrast between Gymnosperms and Angiosperms.—

1. The seeds of gymnosperms are borne upon the surface of the megasporophylls; the seeds of angiosperms are always formed within a closed structure, the ovary, formed by the union of the margins of one or more megasporophylls (carpels).

2. Gymnosperms are all woody, perennial forms, and with few exceptions are evergreen. Angiosperms include both herbaceous and woody plants, and annual, biennial, and perennial forms.

3. In all gymnosperms, except the Gnetales, vessels are lacking, whereas in almost all angiosperms the xylem has vessels.

4. In gymnosperms the pollen comes into direct contact with the nucellus (megasporangium), whereas in angiosperms the pollen comes in contact with the stigma, the tip of a structure (the pistil) consisting of one or more megasporophylls (carpels), which enclose the megasporangia.

5. In contrast to gymnosperms, angiosperms usually have sepals and petals associated with the megasporophylls and microsporophylls, the whole forming a characteristic structure called the flower.

6. In gymnosperms the first divisions of the zygote result in a number of free nuclei; in angiosperms such free nuclear division of the zygote does not occur.

7. The male gametophyte of gymnosperms consists of six cells, whereas that of angiosperms is somewhat more reduced, consisting of but three cells.

8. The female gametophyte of gymnosperms is an extensive tissue consisting of many thousands of cells separated by walls and giving rise to archegonia. The female gametophyte of angiosperms is usually an eight nucleate structure (embryo sac), generally without separating cell walls, which does not produce archegonia but includes one egg nucleus.

9. The more primitive gymnosperms produce motile male gametes; such gametes are not formed in any angiosperms.

10. In the gymnosperm embryo there are normally three to eight cotyledons; in angiosperms either one (in the monocotyledons) or two (in the dicotyledons) is the rule.

CHAPTER XV

EVOLUTION AND HEREDITY

Among the great variety of organisms there are many groups of species which obviously resemble each other more than they do any other kinds of organisms. Familiar examples of groups of similar species which are recognized even by those who are not given to accurate observation of plants are the oaks, all of which bear acorns and most of which have pinnately lobed leaves; the mints, which generally have square stems and whose foliage often has an aromatic odor; the beans, peas, and similar plants, whose fruits are pods or legumes and whose flowers are of a form which suggests a butterfly; and the toadstools and mushrooms with their stalked, umbrella-shaped caps. A careful comparison of the organisms about us would reveal many more such groups of strikingly similar species.

Both the existence of so many different kinds of organisms and the striking similarity between the members of such groups as have just been mentioned demand an explanation. One hypothesis is the **theory of special creation,** which assumes that each species that exists or ever existed was separately created, and that each of the specially created individuals of a species was endowed with the power of producing other individuals like itself, but without ability to give rise to individuals differing from it and thus to form new species. This theory does not furnish any explanation of the close resemblances which exist among certain different kinds of organisms.

A second explanation is the **theory of organic evolution.** This theory had its beginning as early as the time of the Greek philosophers, long before the Christian era. Darwin was one among many scientists of his time who accepted the theory of organic evolution. His special service lay in his attempt to work out the factors in nature by which organic evolution has been brought about.

Evolution is a process in which great differences arise through a succession of slight changes. It is clear that such a process is constantly going on among other things besides plants and animals. History is indeed merely an account of the evolution of human institutions, arts, and practices. Inorganic evolution (the evolution of other things than organisms) is illustrated by the collections which may be found in many great museums showing the history of the development of human apparel, implements of various sorts, optical instruments, etc. During our own lifetimes many of us have witnessed practically the whole course of the evolution of the flying machine and of wireless communication. The geologist can inform us very fully in regard to the evolution of the hills, valleys, streams, and other features of the regions in which we live, and the astronomer knows much of the evolution of our earth and other planets and of the sun and stars.

It is, however, with the evolution of organisms (organic evolution) that we are here concerned. The now generally accepted explanation of the great number of plant and animal species, and of the close similarity existing between some of these, is called the theory of organic evolution.

The principal features of this theory are briefly these:

1. The existing kinds of plants and animals and all the kinds that are now extinct (with the exception of one or a few original and very simple forms) have arisen from pre-existing kinds by relatively slow changes.

2. If the preceding proposition is true, it follows that all the different kinds of plants and animals are related.

3. Those species which are similar in many particulars are closely related, that is, they are not separated by many forms from a common ancestor (species) from which they have descended.

4. Although it is natural to look upon evolution as progressive, that is, as such that it results in an increase in complexity and differentiation, it may often be retrogressive and result in a development of forms having less complexity and differentiation than their ancestors.

If we could secure specimens of all the kinds of plants and animals which now exist or which ever have existed, it should be possible by comparison of their structure to work out the whole

course of evolution. Many species of plants and animals have become extinct. This extinction has in the case of a few species actually taken place since man has been studying plants and animals, and thousands of kinds of organisms died out before the animal species we call man was himself evolved. In the rocks we find the remains of some of these extinct plants and animals as fossils. These remains are in many cases mere fragments of the bodies of these organisms; it is probable that fossil remains of many of these extinct plants and animals, particularly of the simpler and more primitive forms, will never be found.

Heredity and Variation.—There are two remarkable tendencies which are characteristic of all organisms. These two tendencies are **heredity** and **variation**. Heredity may be defined as the tendency of the progeny to be like the parents and therefore to resemble each other. Variation, on the other hand, is the tendency of the progeny to differ from the parents and from each other. It is clear that without variation no new species could ever have arisen from pre-existing species.

That like begets like is one of the most obvious facts in human experience. Even primitive peoples recognize the fact that characteristics are passed on from parents to children and that acorns, the seed of oaks, always grow into oaks and never into pines or apple trees.

However, it is literally true that no two individuals of a species are exactly alike. The familiar expression, "as like as two peas in a pod," which is so commonly used to indicate the closest of resemblances directs the attention of the individual to an excellent example of the dissimilarity (variation) which we find among all plants and animals, for actually no two peas are alike. In fact, every pea in a pod, and even every pea on a plant, is different from every other, and the plants which would develop from these peas, if they germinated, would all show differences in such particulars (**characters**) as size and form of the root system and of the shoot, branching, form, size and arrangement of the leaves, size and arrangement of the flowers, and many other characters.

The question is immediately suggested: Why do the progeny tend to be like the parents and why are they often quite unlike and always slightly different from the parents? The cause can be stated

more briefly and simply in the case of heredity than in that of variation. The progeny generally closely resemble the parents because their living substance was derived from the parents. If the new individuals have arisen by vegetative reproduction, as in the case of stem cuttings and bulb formation, it is clear that all the protoplasm of the new plant came originally from the single parent. In sexual reproduction the new individual develops from a fusion cell or zygote in which are combined a protoplast from one parent with a protoplast, or at least a nucleus, from the other parent. In either case there is continuity of living material from parent to progeny and the tendency to likeness must be due to this continuity. The fact that in many seed plants only the nucleus, and apparently none of the cytoplasm of the male gamete, fuses with the egg cell indicates that at least in these cases it is principally the nuclei which transmit the characters of the parents to the new individual.

Chromosome Theory of Inheritance.—According to this theory it is the chromatin (the material of the chromatin granules in the resting nuclei and of the chromosomes in dividing nuclei) which bears the inherited characters. The number of chromosomes is constant for each species, except, of course, for the fact that the number is doubled at fertilization and halved again at the reduction division. There is very good reason to believe that the identity of these chromosomes is not lost in the period between nuclear divisions, even when they break up into chromatin granules and remain in that condition in the resting nucleus. It is quite certain that with rare exceptions inheritance is due to the continuity of chromatin from one generation to another.

Kinds of Variations.—We recognize three principal kinds of variations in plants:

(*a*) *Modifications.*—These are minor individual variations which are largely due to differences in the soil, moisture, light, or other environmental conditions. If, for example, we planted the seeds from a single self-fertilized wheat plant, the progeny might vary considerably in height of plant, length of heads, and other characters. Such variations, *in as far as they are the result of differences in the environment of the different plants*, are called **modifications**, and variations of this type are probably not inherited.

(*b*) *Mutations.*—Practical growers have observed from time to

time that, among hundreds of thousands of plants of a given strain, there sometimes appear individuals with characters markedly different from those of the general "population" and which breed true for the characters in question. Variations of this kind are called **mutations**, and are popularly known as "sports." As already mentioned, such variations are inherited, presumably because some change in the chromatin has accompanied their appearance, whereas modifications are not inherited and probably are not connected with any change in the chromatin of the nuclei. The red sunflower, the bush Lima bean, and the Concord grape are examples of mutations. No doubt there appear from time to time in many of our fields of cultivated plants such new forms, that is mutations, and if we have an eye trained to distinguish such forms we may be able to discover a valuable mutation which can then be propagated and grown in large quantities.

Sometimes bud mutations or bud sports occur. Thus there may occur on a fruit tree a single branch (developed of course from a single axillary bud) which bears fruit differing in some particular from the other fruit on the tree. If the qualities of the fruit of this "bud mutant" branch are desirable, buds may be taken from the branch and used for budding, thus multiplying the bud mutation. In this connection it should be borne in mind that the bud mutation arises with the formation of a lateral bud, presumably through some change in the chromatin when this bud originated from the promeristem. The whole branch developing from the mutant bud has the characters of the bud sport. Certain varieties of the navel orange and of the Boston fern are examples of bud mutations.

The material substance in the chromosome which determines or conditions one or more hereditary characters is called a **gene.** It seems probable that a gene is a very complex molecule or group of molecules with the ability to reproduce. It is now known that new genes and new arrangements in the chromosomes may arise suddenly owing to chemical and physical changes in the chromatin of the nucleus. Thus there may be gene mutations in plants. For example, many of the varieties of sweet peas have arisen from a single wild species through gene mutation, and subsequent hybridization.

There are many types of chromosome changes. Our attention has been called to the fact that each of the species of plants and animals has a specific number of chromosomes. We speak of these as diploids, meaning that they have two sets of chromosomes. However, it is not rare to find individuals with more

than two sets of chromosomes. Such plants are called polyploids. Polyploids may be triploids (three sets of chromosomes), tetraploids (four sets of chromosomes), hexaploids (six sets of chromosomes), etc. For example, in the cultivated raspberry there are 14 chromosomes, which means two sets of 7 different chromosomes. Among other cultivated forms of the genus *Rubus* (raspberry, etc.) the Mahdiberry has 21 chromosomes, or three sets of 7 different chromosomes (triploid), the Veitchberry, 28 chromosomes, or four sets of 7 different chromosomes (tetraploid), and the loganberry, 42 chromosomes, or six sets of 7 different chromosomes (hexaploid). As another example, the *gigas* mutant of *Oenothera lamarckiana* has 28 chromosomes instead of the normal 14 chromosomes. These so-called "tetraploid" *gigas* plants are larger than the normal or "diploid" plants. Generally speaking, polyploid forms are characterized by their large size and vigor. A considerable number of well-known varieties of flowers and fruits are triploids. For example, the apple varieties, Baldwin, Ribston Pippin, and Gravenstein are triploids; and certain giant forms of tulips and hyacinths are triploids, and have largely displaced the diploid varieties from cultivation.

Various methods have been employed to induce gene mutations and thus secure new sorts of plants. The most common method is the exposure of the seeds to x-rays.

The induction of polyploid plants by various artificial means has also been attempted. Decapitation or wounding of the plants has in certain cases resulted in a doubling of the chromosomes. For example, young diploid (24 chromosomes) tomato plants were decapitated. Adventitious shoots arose from the wound callus, some of which were tetraploids (48 chromosomes). These tetraploid shoots were distinctly different from diploid shoots, in general being more robust and darker green. Both types of shoots can be propagated vegetatively. Recently, polyploidy has been secured by treatment with the chemical, colchicine. For example, tetraploid forms of tomato, marigold, and carnation have been induced by such treatments. Usually the plants are treated in the early seedling stage. Recently it was shown that when two-day-old seedlings of paddy rice were soaked in 0.05 to 0.1 per cent solutions of colchicine for 21 or 48 hours, the plants that developed were tetraploid instead of diploid. This was determined by counting the chromosomes in the cells of root tips. Polyploidy in alfalfa, barley, wheat, and other plants has been artificially induced by subjecting the plants to fairly high temperatures (30° to 45° C.).

(*c*) *Combinations.*—When plants belonging to two different varieties or species are crossed new variations arise as the result of the combination of the different characters of the parents. Variations of this type are spoken of as combinations, and they will be discussed in more detail in the following paragraphs.

Mendelian Inheritance.—A large part of the work which is being done today on the experimental study of evolution, as well as

of the practical work of the plant and animal breeder, is largely based upon the remarkable discoveries of the Austrian monk, Gregor Johann Mendel. His experiments had to do with the manner of inheritance of certain characters by the individuals resulting from the crossing or hybridizing of two organisms differing in one or more characters. He worked for the most part with the garden pea (*Pisum sativum*).

FIG. 271. Leaf variations in *Artemisia vulgaris*. The leaves in each vertical row are from a single plant and thus show variation in one individual. Thus 1*a* is from near the base of a given plant, 1*b* from about half way up the stem of that plant and 1*c* from near the tip of the same plant. The leaves in each horizontal row are from corresponding parts of three different plants and thus show variations between different individuals. (Redrawn from Clements and Hall's *The Phylogenetic Method in Taxonomy*.)

His discoveries, the outcome of eight years of breeding experiments, were published in an obscure scientific periodical in 1866. Partly on that account and partly because the time was not yet ripe for a proper appreciation of its significance, his work remained practically buried for thirty-five years. In 1900, sixteen years after Mendel's death, his publication was discovered almost simultaneously by three botanists, who had been led by their own studies to conclusions similar to his.

His first experiments were made by crossing two varieties of garden peas, a dwarf variety (20-45 centimeters high) and a tall variety (175-200 centimeters high). That is to say, he grew plants of these two varieties and used the pollen from each to pollinate the flowers of the other variety. Peas were favorable plants for his study because the pea is a species which is naturally self-fertilized. On that account, it was reasonably certain, since the seeds produced naturally by the tall variety and the dwarf variety always produced plants which were respectively tall and dwarf, that the varieties were pure as regards tallness and dwarfness.

Mendel found that, whether he used pollen from a dwarf plant to pollinate the stigma of a tall plant or vice versa, the seeds formed gave on germination only tall plants. In different form, these results may be stated thus: When the dwarf variety was crossed with the tall variety all of the individuals of the first (hybrid) generation commonly spoken of as the F_1 (or first filial) generation, were tall.

In the F_2 (second filial) generation, secured by allowing F_1 individuals to self-pollinate, about one-quarter of the individuals were dwarf and about three-quarters tall. Mendel secured 787 tall to 277 dwarf plants. When the F_2 dwarf plants were self-pollinated, all their progeny were dwarf plants. These dwarf F_2 and F_3 plants were like the dwarf plants which were crossed with the tall plants at the beginning of the experiments and they never gave any tall plants as long as they were bred with dwarf plants. Two-thirds of the tall plants of the F_2 generation (that is, one-half of all the F_2 individuals) when self-pollinated, gave one-quarter dwarf and three-quarters tall plants. (See Fig. 273.) The remaining tall F_2 plants, when self-pollinated, gave nothing but tall plants, which in turn gave nothing but tall plants when self-pollinated. In short, although the F_2 plants appeared to be only of two kinds, dwarf plants and tall plants, there were actually three kinds of F_2 plants.

FIG. 272. Gregor Mendel (1822-1884), whose plant breeding experiments laid the foundation for modern genetics. (From Curtis and Guthrie, *A Textbook of General Zoology*.)

(1) Dwarf plants (about one-quarter of all) which gave only dwarf plants when self-pollinated.

(2) Tall plants (about one-half of all the F_2 plants) which when self-pollinated gave one-quarter dwarf and three-quarters tall plants.

(3) Tall plants (about one-quarter of all of the F_2 plants and in appearance like the other tall plants) which gave only tall plants when self-pollinated.

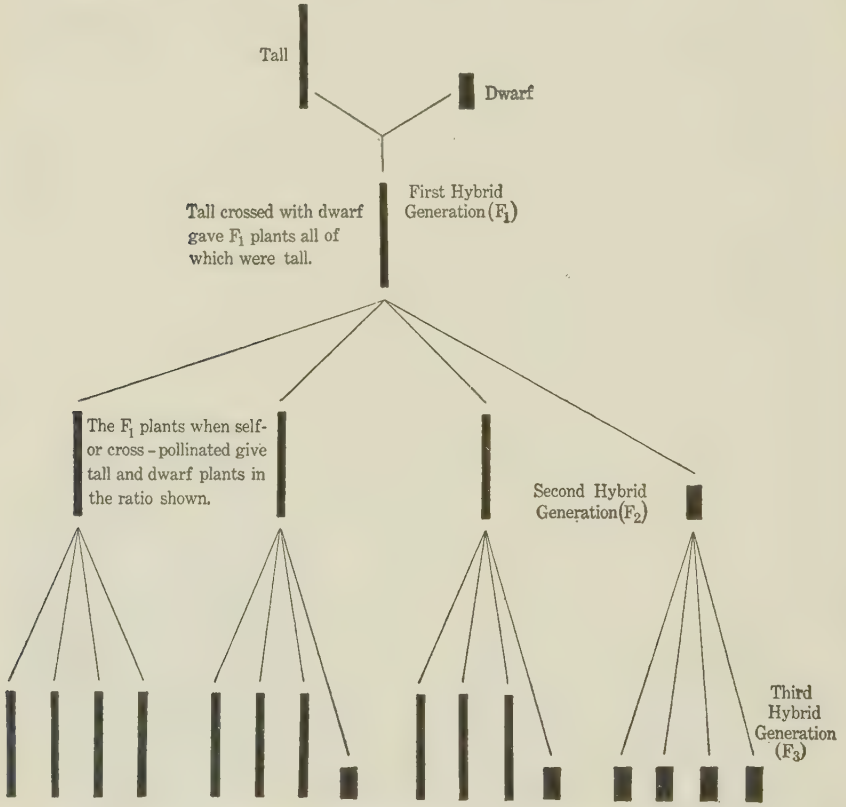

Tall
Dwarf
Tall crossed with dwarf gave F_1 plants all of which were tall.
First Hybrid Generation (F_1)
The F_1 plants when self- or cross-pollinated give tall and dwarf plants in the ratio shown.
Second Hybrid Generation (F_2)
Third Hybrid Generation (F_3)

FIG. 273. Diagram to illustrate inheritance in a monohybrid cross between tall and dwarf peas.

For these three kinds of plants it is convenient to use the following designations, the meaning of which will shortly be made clear: (1) Pure recessives, (2) Hybrids, and (3) Pure dominants.

It is important to bear in mind that the pure recessives, when self-pollinated or cross-pollinated among themselves, never gave

anything but pure recessives, in this case dwarf plants; that the hybrids, when self-pollinated or crossed among themselves, gave the three classes in the proportion 1 : 2 : 1 ; and that the pure dominants, when self-pollinated or crossed among themselves, gave only pure dominants.

Mendel secured results like those just described when he crossed pea varieties having smooth and wrinkled seed coats, and when he used still other varieties characterized by green and yellow cotyledons.

Such characters as those of tallness and of dwarfness in Mendel's peas, when inherited, remain distinct and are thus transmitted as integral units. From the fact that the tall F_1 plants gave some dwarfs when self-pollinated, it is clear that the character for dwarfness was transmitted through the tall F_1 plants as a unit which was not affected by its association with the character for tallness.

One of the most remarkable facts about Mendel's breeding experiments with tall and dwarf peas is that although the F_1 plants had received both the character for dwarfness and the character for tallness, the plants were actually tall; that is to say, the character for tallness prevented the opposite character from coming to expression. Therefore the character for tallness is spoken of as a **dominant character**, and that for dwarfness as a **recessive character**. This prevention of the expression of a recessive character by a dominant character does not always occur in Mendelian inheritance. For instance, when the red-flowered variety of the common garden four o'clock is crossed with the white-flowered variety, the F_1 plants are pink, neither color being dominant.

Explanation of Mendel's Results on the Basis of Chromosome Behavior.—It will be recalled that, with a few exceptions, inherited characters are transmitted from one generation to the next through the chromosomes. That is to say, the progeny have a certain character which was possessed by one or both parents because the nuclei of the new plants contain chromosomes received from the parents. In at least one of the chromosomes of the gametes of each of the original dwarf and tall plants there was a definite and fixed part, or factor, which was the carrier of the character "tallness" in the tall plants and of the character "dwarfness" in the dwarf plants. Similarly for every other character there was present in the gametes

at least one factor in some one of the chromosomes. Now when fusion of gametes (egg and sperm) takes place the diploid nucleus of the zygote will have at least two chromosomes with a factor influencing stature, one from the egg and one from the sperm. Such a pair of chromosomes coming respectively from sperm and egg and each with a factor influencing the same kind of character is called a pair of *homologous chromosomes.*

Now the original dwarf plants which Mendel used for his experiments had in their nuclei no chromosome with a factor for tallness. That is to say, these plants were homozygous for this character,

FIG. 274. Chromosome individuality as shown in *Crepis capillaris* (left) and *C. setosa* (right). The two chromosomes connected by dotted lines to a single Roman numeral are homologous. Each of the chromosomes has already begun to split since the stage of mitosis shown is the metaphase of somatic (2x) nuclei. The chromosomes are shown as seen from a point on the axis of the spindle. Note the similarity in size and form of the two chromosomes in each homologous pair. The use of the same numerals in the left-hand and the right-hand part of the figure is not meant to indicate corresponding chromosomes. (From Collins and Mann, in *Genetics in Relation to Agriculture* by Babcock and Clausen, McGraw-Hill Book Co.)

"dwarfness." Accordingly when they were self-pollinated both the chromosomes of the homologous pair affecting stature had the factor for "dwarfness."

The original tall plants were also homozygous because their nuclei contained no chromosomes with a factor for dwarfness but two homologous chromosomes bearing the factor for tallness. Since these plants are naturally self-fertilized, there is little possibility, under normal conditions, of the introduction of a chromosome with the factor for tallness into the nuclei of the progeny of dwarf plants. Accordingly they produce only dwarf plants (i.e., "breed true").

For the same reason, the original tall plants would also breed true under normal conditions.

In the reduction division, a little before the formation of microspores (pollen grains) and megaspores (one of which gives rise to the embryo sac), the members of each pair of homologous chromosomes are separated from each other and pass to opposite ends of the spindle. Accordingly, the megaspores and microspores (and the same is true of the sperm nuclei and egg nucleus), each contain only one chromosome from each pair existing in the sporophyte nuclei. Since, in the dwarf plants, both the chromosomes of the homologous pair carrying the factors for stature in the sporophyte carry the factor for dwarfness, the egg nuclei and the sperm nuclei are all alike with respect to the factors for statures. Similarly, all the sperm nuclei and egg nuclei produced by the tall plants are alike in that they have the factor for tallness only.

It will make the rest of our explanation somewhat easier to grasp if we substitute the capital letter *T* for the expression "factor for tallness" and the small letter *t* for the expression "factor for dwarfness," the capital letter indicating that the corresponding character is dominant, and the small letter that the corresponding character which it represents is recessive. It will also be convenient to designate the gametes bearing one of these factors as *T* sperm, *T* egg, *t* sperm, and *t* egg, and the zygotes resulting from their fusion as *tT* zygotes, *tt* zygotes, and *TT* zygotes.

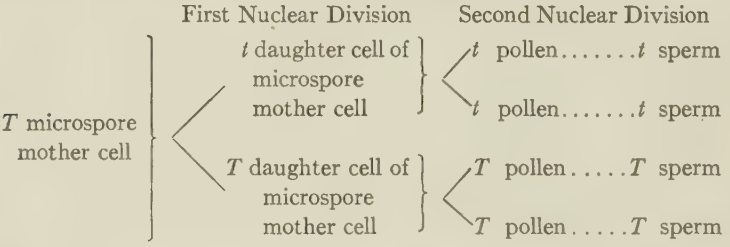
The fact already stated, that Mendel's original dwarf plants bred true, can be restated thus, using the designations just mentioned. *Since, in the case of the sporophytes of the dwarf, both members of the pair of homologous chromosomes controlling stature bear the factor for dwarfness, only* t *sperms and* t *eggs will be produced by the dwarf plants when self-pollinated or crossed with other dwarf plants. Therefore all the zygotes which are formed by the fusion of these gametes will be* tt *zygotes and will give rise to dwarf plants.*

As stated in earlier chapters, the double number of chromosomes in the zygote of any plant consists of pairs of homologous chromosomes, one chromosome of each pair having come from the sperm and one from the egg cell.

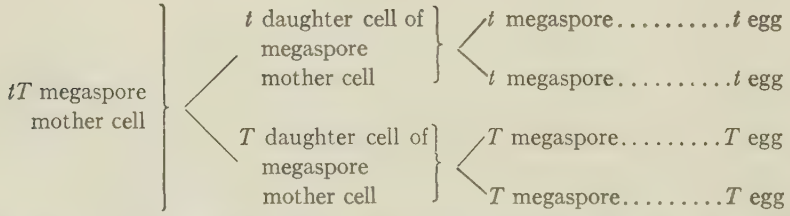
The F_1 Generation.—Now when dwarf and tall plants are crossed, pollen from the dwarf variety may be used to pollinate pistils of the

tall variety, in which case t sperm $\times$ T egg $=$ tT zygote; or pollen from the tall variety may be used to pollinate flowers of the dwarf variety, in which case T sperm $\times$ t egg $=$ tT zygote.

In both cases the zygote contains a pair of homologous chromosomes, each of the members of which bears one of the contrasting factors. Accordingly the F_1 plants developed from the zygotes will be **heterozygous**, and because of the dominance of the tall character will be tall plants. Now at the reduction division of the microspore mother cell, the t chromosome and the T chromosome, which have been associated as homologous chromosomes in all the nuclei of the sporophyte plants, are separated thus:


First Nuclear Division
Second Nuclear Division
tT microspore mother cell
t daughter cell of microspore mother cell
T daughter cell of microspore mother cell
t pollen.....t sperm
t pollen.....t sperm
T pollen.....T sperm
T pollen.....T sperm

As a result, the pollen grains and the sperm cells are of two kinds, T and t, produced in equal numbers. Similarly there are produced T eggs and t eggs in equal numbers, as is shown in the following diagram:


tT megaspore mother cell
t daughter cell of megaspore mother cell
T daughter cell of megaspore mother cell
t megaspore.....t egg
t megaspore.....t egg
T megaspore.....T egg
T megaspore.....T egg

As pointed out on page 345, three of the megaspores are completely absorbed, leaving a single functioning megaspore. In half the cases the functioning megaspore will be a t megaspore and in half the cases a T megaspore, so that the numbers of t and T eggs in the ovaries of the F_1 plants will be approximately the same.

Such separation at the time of the reduction division of the two members of a pair of homologous chromosomes bearing contrasting characters or **allelomorphs**, so that half of the gametes have the

factor for one character and half the factor for the other character, is spoken of as segregation. The resulting purity of the gametes is one of the most important features of Mendelian inheritance.

The F_2 Generation.—Now when an F_1 plant is self-pollinated or cross-pollinated with other F_1 plants, there will be four possible combinations of sperm and egg, since there are two kinds of sperms and two kinds of eggs; and these combinations, by the law of probability, will occur in about equal proportions. These combinations are:

(1) *T* sperm × *T* egg giving *TT* zygote,
(2) *t* egg × *T* sperm giving *tT* zygote,
(3) *T* egg × *t* sperm giving *Tt* zygotes, and
(4) *t* sperm × *t* egg giving *tt* zygotes.

These four combinations and their origin may be shown graphically by the following checkerboard diagram. In this the two kinds of sperms are placed in the horizontal row, the two kinds of eggs in the vertical row, and the possible combinations of gametes are shown in the four squares:

	T	*t* sperms
T	1 *TT*	3 *Tt*
t eggs	2 *tT*	4 *tt*

Let us consider briefly the result of these four combinations as they are expressed in the individuals of the F_2 generation. Combinations 2 and 3 are identical, since in both there is a chromosome bearing the factor for dwarfness and a chromosome with the factor for tallness. Together, these zygotes will make up half of all the zygotes resulting from the cross. They will all form seed which will develop into tall plants because of the dominance of tallness. In fact, these plants are the ones which we designated earlier as the hybrid, F_2 plants. They are identical with the F_1 plants in appearance and in their behavior when interbred, i.e., self-pollinated or pollinated with pollen from similar plants.

The zygotes resulting from combination 4 will develop into homozygous plants for this character, since in this case both the members of the pair of homologous chromosomes governing stature bear the same factor (dwarfness). They will be dwarf plants, since the dominant character is entirely absent, and for the same reason tall plants can never arise from them as long as they are interbred. These are the plants which were designated in an earlier paragraph (page 364) as pure recessive plants. They are indistinguishable

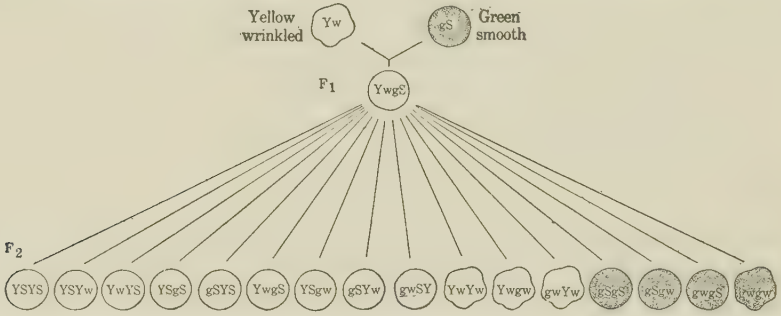


FIG. 275. Diagram to illustrate inheritance in a dihybrid cross between a pea which would have produced yellow wrinkled seeds if self-pollinated and one which would have produced green smooth seeds if self-pollinated. Wrinkled seeds are distinguished from smooth by their outline and green from yellow by the shading of the former. The letters show the various combinations of factors.

in appearance, and in their behavior when interbred, from the original dwarf plants used at the beginning of the experiment.

The zygotes resulting from combination 1 will be homozygous also, and will correspond in their behavior with the pure recessive, except that they and their progeny will all be tall plants instead of dwarf. They are the plants that were spoken of in an earlier paragraph as the pure dominants and are indistinguishable from the original tall plants used at the beginning of the experiment.

THEORIES AS TO THE ORIGIN OF SPECIES

Direct Response to Environment.—According to the theory of Geoffroy St. Hilaire, the French naturalist (1772-1844), new species have arisen in direct response to changes in the environment. That is to say, as climatic and other conditions on the surface of the earth have slowly altered, these changes have called forth variations

in the organism. A succession of such variations in a species might result in a new species. St. Hilaire believed some of these changes to have been favorable, or at least not unfavorable, and that the individuals which underwent these changes survived. Others were unfavorable and resulted in the destruction of the individuals.

Use and Disuse.—Jean de Lamarck, another French naturalist, proposed an explanation of evolution which is commonly spoken of as the theory of "use and disuse." It is a familiar fact that, in the case of individuals, the continued use of a part of the body, as, for instance, the muscles of the arm of a blacksmith, results in a development of that organ which makes it better able to do the work habitually required of it. It is also true that persistent disuse of an organ is apt to result in its partial degeneration or even suppression. Now Lamarck believed that changes in the environment might bring certain organs into disuse and increase the extent to which other organs were used, and thus bring about degeneration of certain organs and build up or modify others. Moreover, he regarded these characters acquired during the life of an individual as heritable. Thus the environment might, by reduction or suppression of certain organs and development of others, cause new species to arise.

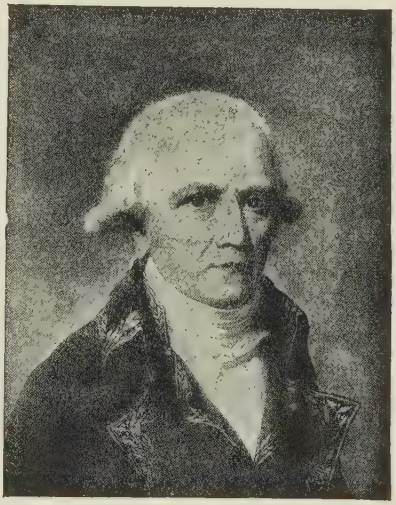


FIG. 276. de Lamarck (1744-1829), an early evolutionary biologist best known for his theory of the inheritance of acquired characteristics. (From Shumway after Pirsson and Schuchert.)

Lamarck's theory was founded on three assumptions: (1) that the environment changes, (2) that use and disuse may alter the character of an individual, and (3) that the variations thus acquired can be inherited. The first two assumptions are recognized as correct, but there is no convincing evidence to indicate that acquired characters (modifications) can be inherited.

Orthogenesis.—Another theory, which has been advanced by different men and in different forms, is that there is inherent in every

species a tendency to vary in a certain definite direction. If variation in this direction does not result in the individuals becoming less favorably adapted to their environment, new species will arise and these in turn will give rise to others. Otherwise the variations will not persist. The principal objections to this theory are: (1) It has never been shown that such a persistent tendency to vary in a certain direction exists. (2) No explanation has ever been given as to the driving force or principle which is responsible for the assumed tendency.

Darwin's Theory of Natural Selection.—The most famous of the theories of evolution is Charles Darwin's theory of natural selection. The principal features of this theory are:

1. Plants and animals in nature produce many more progeny than can possibly survive.

2. Because of this production of individuals far beyond the earth's facilities to support them there is a struggle for existence.

3. Individual organisms differ in their fitness for a given environment.

4. Through the struggle for existence there is a natural selection which results in the survival of the fittest or, to put it conversely, in the destruction of the unfit.

5. The individuals of a species are not at all alike and even among the progeny of the same parents there are always at least slight variations.

Illustrations of the kind of variations which, according to Darwin, provide the material for natural selection can be secured by measurements of any plant or animal structure in many individuals of a given species. Thus if the length of all the bean seed in a lot is measured, and if all those having approximately the same length are sorted out, the following relation will be found to exist: The number of the beans having the least length will be very few. Those having the greatest length will also be very few. Between these extremes the numbers will increase as we approach the length halfway between the two extremes, at which length or near it we will find the largest number of individuals. The variations in question are often spoken of as fluctuating variations and probably include cases of the nature of both modifications and combinations. If the variations can be inherited it is possible, by selecting through some

generations, to increase the average length of the beans. Thus the length characteristic of the greatest number of beans in any generation would be displaced in the direction of the extreme length. There is no reason, however, for believing that the extremes would change. Instead, the greatest length and the shortest length would

FIG. 277. Charles Darwin.

Reproduced from the *Beagle Diary* by permission of the Cambridge University Press and Professor A. C. Seward.

remain the same, and unless the extremes of variations can be shown to be changed by selection nothing new has been produced. The mere increase in the relative number of individuals varying in a given degree, which degree of variation already existed, cannot account for the origin of a new species. In short, there is some question whether natural selection of fluctuating variations can push

the range of variation beyond certain limits which are characteristic of a species.

Another objection to Darwin's theory of the origin of new species is that the variations involved seem for the most part to be too small to be of life and death importance to the organism and to be the basis of natural selection.

The Mutation Theory of Evolution.—Hugo de Vries, the great Dutch student of mutation, suggests that new forms originate by mutation rather than by fluctuating variations. The principal features of the mutation theory of evolution are the following: (1) There arise from time to time, among the individuals of a species, forms which differ relatively widely in one or more characters from typical individuals. (2) The characters of these variations (mutations) are inherited, at least in many cases. (3) These mutations arise quite independently of fluctuating variations. (4) Mutations may take place in any direction. (5) The mutants (mutating individuals), at least in many cases, differ sufficiently from typical plants to make them subject to natural selection. (6) Accordingly, in nature all unfit mutants are likely to be eliminated by natural selection.

The uncertainty which exists as to the method by which new species arise is not to be interpreted as indicating any serious doubt on the part of biologists that new species do arise by natural processes; in other words, that evolution does take place, although how it operates is not yet entirely clear.

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